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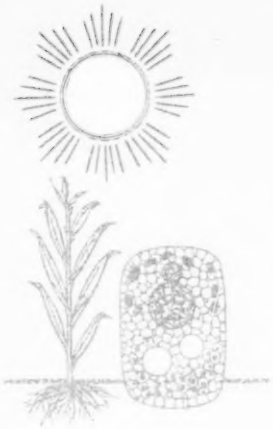
A New Era In Pest Control: THE STERILITY PRINCIPLE PAGE 2



AGRICULTURAL SCIENCE REVIEW
Fall 1963 Vol. 1, No. 1

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The Language of Science

Probably no other form of communication faces greater innovations in the years ahead than does the language of science. True, its traditional characteristics—pure objectivity, lavish use of technical terms, and symbolic statement of fact—are likely to remain, or perhaps become even more dominant when scientists are sharing knowledge among themselves. But because science and its product affect interest groups outside the realm of the laboratory, its communications patterns will, at times, need to be modified.

Of highest priority is the need for a better public understanding of science knowledge. Surveys have revealed wide areas of ignorance about modern technological concepts. Such ignorance is detrimental both to the public welfare and to the scientific community itself. Much of the burden for correcting this situation rests with scientists themselves. Only when they learn to adapt their language at the right time and in the right way can the myths and misunderstandings surrounding the research laboratory be dispelled.

Almost equally important is the need to establish a more effective crossfire of disciplines; that is, the interaction of every branch of science with other branches. This interdisciplinary communication depends heavily on the use of a language geared to the premise that every science author is somewhat of a layman for articles in fields other than his own.

Finally, the language of scientists must be adaptable to the language of professional documentalists—those who are skilled in the mechanical techniques of information transfer. Authors will need to assume more responsibility for the final links in the dissemination process by preparing manuscripts, abstracts, and titles that enable documentalists to store and retrieve the information quickly and accurately. The benefits such cooperation affords are too valuable to be overlooked.

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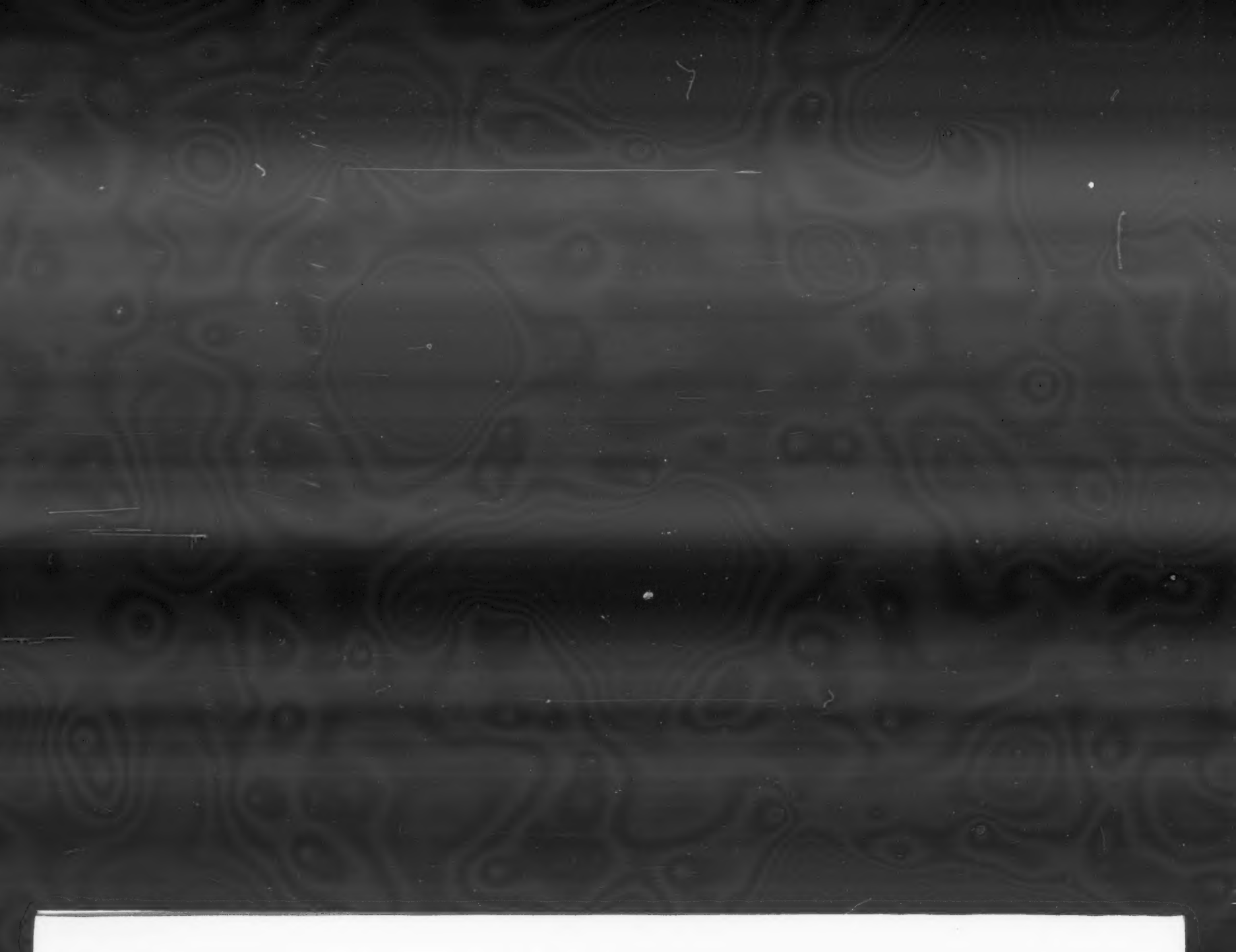


AGRICULTURAL SCIENCE REVIEW -Its Purpose and Goals

T. C. Byerly, Administrator, Cooperative State Experiment Station Service

NEVER before in history has the scientific community concerned with agricultural research encountered more complex problems in the sharing of technical knowledge. Two factors—the mass communications media and the burgeoning hosts of research scientists—have brought us a veritable "Babel of words" that threatens the unity of science literature.

No one can question the need for this new knowledge. But who among us can hope to find, read, and assimilate it from the original sources?

This, therefore, is the picture as *Agricultural Science Review* publishes its first issue with the modest hope of more effectively communicating the achievements in agricultural science.

The new periodical in no way resembles either the *Experiment Station Record* or the *Journal of Agricultural Research,* both of which served their purposes well in another era. In contrast, *Review* will publish no primary research reports. Emphasis will be heavy on critical, comprehensive review papers that synthesize accomplishments in specific areas of research and identify problems and needs. Such reviews are urgently needed to provide a common point of understanding among scientists from every discipline.

It is our hope that *Agricultural Science Review* will facilitate planning and coordination of information on research related to agriculture by providing an authoritative commentary on published research, research in progress, and trends in research. Moreover, a ready and reliable source of information on the current state of agricultural science, we believe, will assist in promoting the quality of research management.

From time to time, *Review* will publish articles that analyze areas and problems of particular concern to the administration of research. At this level, because of interrelations between agencies and between disciplines, the coordination of technical knowledge is vital to achieving maximum benefits from available resources.

We realize that the objectives of *Review* touch on only one facet of the current information problem. Much remains to be done in mechanizing the storage and retrieval of knowledge. But within the framework of new concepts, the role of the critical reviewer takes on a new and more important dimension. This fact has been stressed heavily by the President's Science Advisory Committee.

From a broader viewpoint, one of the goals of the new periodical is to give other areas of science a better understanding of agricultural research as a significant force in the growth of civilization. Man can never disassociate the fruits of the soil from his own welfare, nor from his pursuit of knowledge in other areas.

Review will seek its authors from among those best qualified to speak for agricultural research—active scientists and administrators, the theorists, the documentalists, the teachers—wherever they may be. The Editorial Board will recommend to the Editor desirable topics and the names of research workers best qualified to prepare manuscripts on these topics. Proposals for topics and authors will be welcome. Beginning with a limited distribution of four issues a year, we expect to broaden the scope of the new periodical eventually so that it will serve the disciplines more fully.

Our staff and the Editorial Board welcome your thoughtful suggestions for a better periodical. We earnestly seek your support. If the articles in this issue and succeeding issues can excite inquiring minds and can accurately reflect the changing needs and problems of research and development, *Agricultural Science Review* will assuredly become a viable influence in the scientific community.

A New Era In Pest Control:

THE STERILITY PRINCIPLE

E. F. Knipling

USING the sterility principle for the self-destruction of insects represents a method of control that could be tremendously important in meeting insect pest problems in the future. Thus far the principle has been considered primarily for controlling or eliminating insect populations. It should offer similar opportunities for regulating vertebrate pests.

The release of sterile insects has been used successfully only for controlling the screw-worm, which was eliminated from the island of Curaçao in a pilot eradication effort by the Entomology Research Division. Results of the basic laboratory and field studies have been reported in various publications by R. C. Bushland, A. W. Lindquist, A. H. Baumhover, and their associates in the Insects Affecting Man and Animals Research Branch. A successful eradication program in the Southeast by the U.S. Department of Agriculture and the Florida Livestock Board followed the Curaçao experiment. An extensive and more difficult program sponsored by the U.S. Department of Agriculture and the Southwest livestock interests is currently underway to eliminate the screw-worm from its normal range in southwestern United States. If the eradication phase is successful, efforts will be made to prevent its reestablishment by the continuous release of sterile flies in a barrier zone along the Mexico-United States border.

The Entomology Research Division, ARS, has intensified its research efforts during the past decade—largely at the expense of other phases of research—to explore the potentialities of the sterility principle for controlling or eliminating certain other insect pests. Despite limited research resources for such work, progress has been excellent. Results to date on several important insect species have shown sufficient promise to suggest that research on this approach to pest control warrants major attention and support.

Research is underway on two ways of utilizing the sterility principle—the rearing and release of large numbers of sterile insects which compete with normal insects in the population, and producing sterility in the natural population. This latter method would obviate the need for rearing and releasing sterile insects.

Each method involves the use of insects for their own destruction, but there are important differences between the two methods in the way that the sterile insects affect population trends. Much research must be conducted and many problems must be resolved to realize the full potential that the two sterility methods hold. Basic information is needed

on many aspects of the biology, ecology, behavior, genetics, rate and distance of spread, and population dynamics of insects that formerly seemed to be of little consequence, and hence is now generally lacking. This is true even for some of our most destructive species that have been the subject of extensive research for many years. Moreover, our entire concepts of how to deal with pest problems must change if we are to take advantage of the methods. We must give primary attention to the pest population when it is at its lowest level rather than when it is at its highest level. We must think in precise quantitative terms in regard to such pest populations. We must think in terms of the total pest population in a community, region, or nation, and not just segments of the population on individual farms.

The sterility principle will not be applicable for all insects or even a majority of the destructive species. It could, however, play a vital role in meeting many of our major insect problems. There are indications now that the method may be feasible to help eradicate or control a number of key insects and future developments should broaden its potential usefulness.

BASIC PRINCIPLES IN STERILE-MALE RELEASE METHOD

Theoretical Aspects

THE effective use of sterile insects for release depends on our ability to rear enough insects to overflood the natural population. The insects to be released must be made sterile without seriously affecting the ability of the released males to compete with normal males in the natural environment. The number of insects required, the allowable cost of rearing them, and the required ratio of sterile to fertile insects—all depend on the species and the circumstances. Where both the natural population density and the biotic potential for the species are high, billions of insects may be needed. The natural population, initially, would have to be overflooded by a factor of 25 or more. For the procedure to be practical under such circumstances, it will of course be necessary to develop very low cost methods of rearing and distributing the many insects required. In many situations, however, the natural population density of the pest may be low. Here, relatively few sterile insects might be adequate and the allowable cost for rearing them may be high.

If fully competitive sterile insects are released, we can make a reasonably valid estimate of the effect such releases will have on population trends, provided that we know the natural population density level and the normal rate of increase from one generation to the next. Table 1 shows the theoretical trend of an insect population subjected to the release of a constant population of sterile insects each generation.

The assumption is made that the normal uncontrolled population is increasing at the rate of fivefold per generation, which is probably fairly realistic for many insect species even though the biotic potential is much higher. It would be necessary, therefore, to overflood the natural population by at least 4 to 1 to prevent an increase in the natural population. To start a downward trend, the initial release rate would have to exceed 4:1. To start a downward trend with a chemical, the level of kill must exceed 80 percent. The model provides for an overflooding ratio of 9:1 for the initial generation so that a downward trend in the population will result. The degree of control with the insecticide is assumed to be 90 percent each generation. Thus, the effect on the reproductive potential of both populations would be the same for the first generation.

Note, however, that with the sterile male method, a constant release rate will result in a higher and higher ration of sterile to fertile insects as the population declines. The effect on the population trend becomes progressively greater each generation. On the other hand, the effect of each insecticide treatment on the population trend remains constant regardless of the population density. When the population density is high, the insecticide treatment is highly efficient in terms of the actual number killed. But the efficiency of each treatment becomes lower and lower as the population declines. These are features of major significance in considering the role that insecticides and the release of sterile organisms might play in meeting pest problems.

In most situations, the natural population of a pest, even at the lowest level in the population density cycle, may be so high that it would not be practical to rear and release enough sterile organisms to start a downward population trend. In

TABLE 1.—THEORETICAL MODEL SHOWING THE TREND OF INSECT POPULATIONS SUBJECTED TO 3 TREATMENTS

Generation	No treatment	Insecticide treatment that kills 90 percent each generation	Release of constant number of sterile insects that initially overflood the natural population by a ratio of 9:1			
			Natural population	Sterile population	Ratio: Sterile to fertile	Progeny
	Number	*Number*	*Number*	*Number*		*Number*
Parent	1,000	1,000	1,000	9,000	9:1	500
F_1	5,000	500	500	9,000	18:1	132
F_2	25,000	250	132	9,000	68:1	10
F_3	[1] 125,000	125	10	9,000	900:1	0
F_4	125,000	62	0			
F_5	125,000	31				
F_6	125,000	16				
F_7	125,000	8				
F_8	125,000	4				
F_9	125,000	2				
F_{10}	125,000	1				

[1] An uncontrolled population of any insect will reach a maximum population level that the environment will maintain. For this model, it is assumed that 125,000 would represent the maximum.

such event the prior use of an insecticide or some other method of control would be more efficient and practical than the release of sterile organisms. However, the release method should become more practical than insecticides at some point in the natural population density level. We may illustrate this by citing some hypothetical figures. A 90-percent kill of a million insects in a population by an insecticide would mean the destruction of 900,000 insects the first treatment. In terms of numbers killed, this would be highly efficient. The second treatment, however, would destroy only 90,000; the third, 9,000; the fourth, 90; the fifth only 9. Thus, as the population declines each insecticide treatment becomes less efficient in terms of the number of individuals killed.

At some point in the population density level, the rearing and release of sterile insects should become more efficient and perhaps more desirable than the continued use of an insecticide. The density level at which the rearing and release of sterile insects will become more efficient than insecticides will depend on the cost of producing the insects.

In general, we might conclude that a combination of the two systems of insect control in many situations would be highly complementary and more effective, more economical, or more desirable than either system alone. Once the population of an insect reaches the manageable level with sterile insects, each sterile male insect is not only a survey tool but also a lethal weapon. If an area under treatment is subject to reinvasion of normal insects, relatively low level releases of sterile insects on a continuing basis may be adequate to prevent reestablishment and thus provide continued control more economically than the routine use of chemicals.

Keep in mind that the effect on population trends as depicted in the model is hypothetical. Research on several insect species, however, has confirmed the principle.

Progress and Problems

As previously indicated, the screw-worm is the only insect in which the release of sterile insects has been actually employed for insect eradication. Substantial progress has been made, however, in developing the principle for other insects. We now face several problems. First, a suitable method of inducing insect sterility must be developed. Presently, the Entomology Research Division is conducting extensive research on gamma radiation and chemosterilants. Studies with radiation sterilization have shown wide variation in the effect of gamma rays on different insect species. In all insects, substantial reduction in sexual vigor and competitiveness due to radiation is apparent. With some insects, however, vigor is reduced to such degree that the males are of little value. The screw-worm, tropical fruit flies, the codling moth, and certain other insects can be radiated in the pupal stage without serious adverse effects. Radiation effects are severe on the boll weevil, the sugarcane borer, the gypsy moth, and the European corn borer. The adverse radiation effect on the pupal stage of some insects is largely morphological, as in moths that emerge from pupae with deformed wings. In such species, radiation of the adult stage may reduce the serious damage to the wings.

Although atomic radiation may prove to be the most desirable way to sterilize certain insects, chemosterilants seem to achieve sterility in insects with less adverse effects on the competitiveness of the males. The Orlando, Fla., laboratory has pioneered the early investigations on insect chemosterilants that will produce sterility in both sexes of insects. The Pesticide Chemicals Research Branch has given major attention to the chemical aspects of research on chemosterilants. In addition, the Division's laboratories at Mexico City, Mexico; Kerrville, Tex.; and Corvallis, Oreg., as well as a number of other locations have evaluated chemosterilants on a wide range of insect species.

Research thus far indicates that chemosterilants could be used to sterilize such insects as the house fly, several species of mosquitoes, all of the species of tropical fruit flies, Drosophila fruit flies, codling moth, pink boll worm, boll weevil, tobacco budworm, tobacco horn worm, as well as others. Much remains to be done on all of these insects and other species. But the ability to release reasonably competitive sterile insects does not appear to be a major obstacle to the development of the sterility principle for practical use.

Mass Rearing of Insects

The ability to rear insects in sufficient numbers and at a cost that will be practical appears to be feasible for many insects. During recent years the Entomology Research Division has given high priority to research in this area, not only in relation to the sterility method of control but also for other reasons. Remarkable progress has been made in the mass production of such insects as the screw-worm, four species of tropical fruit flies, Drosophila fruit flies, the tobacco hornworm, and several species of biting flies and mosquitoes. Although much additional research is needed, excellent progress has been made in developing mass rearing methods for such insects as the boll weevil, pink bollworm, cabbage looper, tobacco budworm, codling moth, European corn borer, and other species.

Currently the cost of producing screw-worm flies in the Mission, Tex., rearing plant probably is within the range of $250–$300 per million insects. Tropical fruit flies such as the oriental, Mexican, Medfly, and melon fly probably could be mass produced at a cost ranging from $100–$200 per million. A cost factor ranging from $1,000 to $5,000 per million may be practical for a number of insects. This depends on the situation under which sterile males might be used as an adjunct to other methods of control.

One of the essential requirements in appraising the feasibility of utilizing sterile male insects is knowledge of the natural population density of the insects to be controlled. Such information must be available on a quantitative basis. For well-established insects, we can assume that the natural population density in most areas will be too high, even at the lowest density level, to utilize sterile male releases alone for practical control. However, a pertinent question is: To what extent is it feasible to lower the population by other methods of control to a level that could then be dealt with by the release of sterile insects? Research has been undertaken on a number of insects to obtain such information.

It seems entirely possible that the boll weevil population can be reduced readily to a level of 5 to

10 adults per acre by the use of insecticides in a spring or fall treatment program. At this low level, it should become entirely feasible and practical to overflood the natural male population with sterile males by a ratio of from 25 to 50 times at a cost that would be no higher than the cost of continued use of insecticides to further reduce or prevent the buildup of boll weevil populations. If the natural population of boll weevils is reduced to 5 males per acre, the addition of 200 sterile males per acre per week would cost only $1 per acre if a production cost of $5,000 per million insects could be achieved. This would be a lower cost than the application of insecticides each week.

Research on population densities, the expected rates of increase from one generation to the next, the dispersion habits, the ecological requirements, and many other aspects of insect population dynamics and insect ecology which are of vital importance in applying the sterile male principle is difficult and costly. But only through such research will it be possible to appraise the potential possibilities of the sterile male release method for controlling or eliminating insects that are already well established.

Status of Research

ASIDE from the screw-worm, the greatest advance in research on the sterile male release method has been made on tropical fruit flies. A pilot experiment to eradicate oriental fruit flies on the island of Rota was not successful, because it was not possible to achieve and maintain the desired ratio of fully competitive sterile to fertile flies with the research resources available. There are circumstances in which the method would undoubtedly be entirely feasible and advantageous alone or in combination with other methods.

An experiment just completed on Rota with sterile melon flies has led to the eradication of this important vegetable pest. Eradication was achieved within about 3–4 months after releases began. The natural population was first reduced by applying bait sprays to restricted areas of high population densities. A ratio of about 15 sterile to 1 fertile insect was achieved within a month; this quickly rose to over 100 to 1 in about 2 months. Eradication soon followed. This is the first multiple-mating species in which eradication has been demonstrated by the release of sterile male insects.

A pilot experiment on the island of Hawaii, conducted in a semi-isolated area, demonstrated that Medfly population could be reduced by the sustained release of sterile males. Research has advanced to a stage that practical eradication experiments on the Mediterranean fruit fly are justified.

Several pilot experiments in semi-isolated areas in Mexico have shown that Mexican fruit fly populations can be held down by the release of sterile males. Practical eradication experiments in completely isolated areas are indicated and are planned.

Canadian workers have shown in laboratory and caged tree experiments that the reproductive potential of the codling moth can be greatly reduced by the presence of sterile male codling moths. Research on methods of mass producing codling moths and various ways of sterilizing the insect is underway at the Division's Yakima, Wash., laboratory.

Studies show that a high ratio of sterile to fertile boll weevils will eradicate an artificially induced infestation in the field. A pilot eradication effort will be undertaken within 1 or 2 years. Prior reduction of the natural population with insecticides will be required. Much research is still needed on the boll weevil to develop better methods of inducing sterility. However, the practical use of sterile boll weevils to eradicate low level populations seems encouraging.

Research on the tobacco hornworm indicates that the sterile-male method might have a place in the control of this insect. Several islands in the West Indies have been surveyed and plans are underway to initiate a pilot eradication effort within the next year.

Research on Drosophila fruit flies has shown that the natural population can be reduced by the release of sterile males. Pilot experiments are planned to determine if field control can be achieved by sterile male releases.

Research on the pink bollworm has advanced to a stage that a pilot eradication experiment in an isolated area is warranted for this important cotton pest.

Additional research is still needed on various aspects of the problem before it can be determined that sterile insect releases will be effective as a means for controlling or eradicating low level populations of the various insects mentioned. However, excellent progress has already been made and the outlook

is encouraging for developing practical ways to use sterile insects for such purposes.

EXAMPLES OF POSSIBLE APPLICATION

OUR numerous insect problems and the many and varied circumstances when eradication is necessary or desirable will suggest many situations where the release of sterile insects should prove advantageous over existing eradication methods.

1. The **Mexican fruit fly** is a continuing threat to California fruit and vegetable interests because of the spread from the border city of Tijuana in Mexico. The threat results largely from flies emerging from infested market fruits grown in other areas in Mexico where the fly is established. The total number probably does not exceed 1,000 each year. If periodical releases of sterile Mexican fruit flies totaling 1 million flies were made each year along the United State-Mexican border, a ratio of perhaps 1,000 sterile to 1 fertile fly could be maintained at all times. There is every reason to believe that such high ratio of sterile to fertile insects would provide adequate security against establishment of the insect in southern California. The cost of rearing 1 million Mexican fruit flies probably would not exceed $200. The current method of applying sprays is not only many times more costly, but for various reasons frequent application of insecticides over a period of years has several undesriable features.

2. A recent establishment of **pink bollworms** in Arizona necessitated a costly eradication program in a 75,000-acre area. Pink bollworms were numerous in much of the area before the eradication began; intensive use of insecticides during the first year greatly reduced the size and extent of the infestation. During the second year about 32,000 acres were treated at a cost of about $700,000. However, the number of pink bollworms found and moths trapped totaled less than 100. The natural population density of the pink bollworm is unknown, but for the first generation during the second year the number may not have exceeded 1 million.

If the sterile-male method had been perfected for pink bollworm eradication, as few as 100 million sterile-male moths might have been adequate to eliminate the low level infestations during the second and subsequent years. If mass production of pink bollworms could be perfected at a cost of $1,000 per million—which should eventually be possible—the use of sterile males in such situations would have cost only $100,000. Not only would such cost be less than that of current methods, but it would obviate the need for high accumulative rates of insecticides in the treated area. The sterile-male method might make it more feasible and practical to eventually initiate a program to eradicate the pink bollworm from the United States by using both chemical and cultural methods to reduce the populations to levels that can be managed with sterile males.

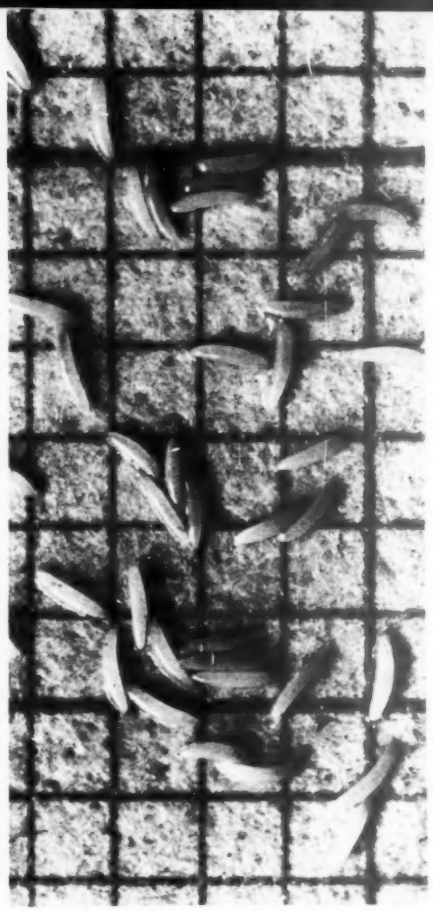
3. A recent **Mediterranean fruit fly** introduction in Florida was discovered when the natural population probably did not exceed 1 million. A total of 64 adults were caught in traps. Again, it is not possible on the basis of current knowledge to translate such trap collection figures in terms of total population in the area. However, the estimate of 1 million is probably conservative. If the sterile-male method were fully perfected, it is possible that the infestation could have been eradicated by releasing several hundred million flies over a period of a year or so. The bait spray treatment now used was applied on about 80,000 acres—over 700,000 accumulative acre applications. The total cost was about $800,000. Mediterranean fruit flies could no doubt be

produced at a cost of about $200 per million. Even if 1 billion sterile flies would have been required, the estimated cost of $200,000 for sterile flies would be substantially less than the current bait spray method.

4. The **Japanese beetle** poses a difficult problem of eradication when infestations are discovered in new areas, even though the total acreage affected and the number of beetles present generally are small.

No research has been undertaken on ways to induce sterility in Japanese beetles, and mass production methods for the insect have not been developed or investigated. New beetle infestations, however, are often detected when the number of insects does not exceed more than a few thousand. If rearing costs could be developed at a figure of $10,000 per million—a cost figure which probably could be readily achieved—1 million sterile Japanese beetles might suffice over a period of a few years to eliminate many small initial infestations that would cost much more to eliminate with insecticides. Moreover, the undesirable side effects of current eradication procedures could be avoided. Liberating adult Japanese beetles might pose some threat to certain crops, but the number required might be below the level that would cause significant crop damage. When new infestations cover rather large areas, such as the current one in Michigan, the use of insecticides in the more heavily infested areas and the use of sterile-male beetles in fringe areas might substantially reduce the area requiring insecticide treatment. Also, following the use of insecticides, low-level populations may survive. These are difficult to deal with and may require extensive surveys and followup treatments with insecticides. The release of a few million sterile males in such areas could mean the difference between success and failure.

5. Sugarcane growers in Louisiana annually spend about $1 million to control the **sugarcane borer.** Under normal circumstances the population density of the insect in the spring is probably too high to use sterile insects alone for control or eradication. During 1962–63, however, cold weather reduced the population to about 50 larvae per acre. If satisfactory methods of inducing sterility could be achieved, and if rearing methods could be developed at a cost of about $1,000 per million, the sterile-insect method of control might be set



up under similar circumstances at an overall cost less than that generally required for insecticidal control. Once virtual elimination is achieved, continued release of sterile males at very low levels each year might prevent reestablishment of damaging populations. The 1963 spring population of moths in the 300,000 acres of sugarcane in Louisiana probably did not exceed 25 per acre, or 7½ million moths. If 100 million sterile moths were required for each of three generations, it would be necessary to produce and release 300 million moths the first year. This number of insects may seem large, but at an estimated production cost of $1,000 per million, the cost of producing the insects would be $300,000. The cost of insecticides for the control of sugarcane borers amounts to about $4.50 per acre per year—or about $1,350,000 for 300,000 acres.

6. Insecticide sprays are highly efficient for the destruction of **gypsy moths.** In actual eradication efforts against isolated infestations, it is common to find a very light infestation surviving either in

the treated area or just outside of the treated area. The number of moths responsible for the continuing infestation may not exceed more than a few thousand. Yet, it may be necessary to treat thousands of acres the second year to complete eradication. If moth rearing and ways of providing sterility could be perfected, sterile males should prove useful for final eradication and perhaps for fringe-infested areas and buffer areas with substantial reduction in the acreage requiring treatment with insecticides. It would seem reasonable to estimate a cost of $10,000 for the rearing and release of 1 million sterile-male gypsy moths.

An eradication effort now underway in New Jersey is an example where the sterile-male method might have been useful. According to discussions with the Plant Pest Control Division, ARS, the infestation of gypsy moths currently present in New Jersey may require spray treatments on about 70,000 acres at a cost of over $100,000.

Trapping and egg mass surveys have yielded less than 100 moths and egg masses. Again, it is not possible on the basis of current knowledge to translate survey records into natural population density estimates. However, if we assumed that the total moth population in the area would not exceed 10,000 (5,000 males and 5,000 females) and if the release of 1 million sterile males each year for several years would assure the elimination of such light infestation in the 70,000-acre area, the cost would be substantially less than the insecticide treatment. Moreover, the sterile-male method would also avoid the objections that arise from insecticidal application.

If the 10,000 estimate for the natural population density is reasonably valid, the release of 1 million male moths would constitute an initial ratio of 200 sterile males to 1 fertile male. Such ratio of reasonably competitive sterile moths should substantially reduce the infestation the first year. If releases were continued for 1 or 2 years, the moths should be eradicated. Entomologists with the Forest Service are conducting investigations on the sterility method for gypsy moth eradication. The eradication problems posed by this insect would seem to fully justify a major research effort to explore the feasibility of using sterile males in future situations such as that in New Jersey.

Other examples could be cited where the sterile-male method could prove advantageous over current methods of control or eradication, or where it could provide an important supplementary method. The insect problems cited are realistic. But the feasibility of using sterile insects to meet them is still speculative. Nevertheless, there is good reason to believe that the principle of using sterile insects could be developed if research were adequately supported.

It is obvious that extensive and costly research will be required to develop the sterile-male release method for each insect where the method may be practical alone or integrated with existing control methods. However, in view of the growing concern over the potential adverse effects of some of the current methods of meeting many of our major insect problems and the continuing economic loss caused by many of our major pests, there is every justification for enough research support to fully appraise the feasibility and merits of the sterility method for all of the major insect pests where there is any indication that success could be achieved.

BASIC PRINCIPLES IN USE OF CHEMOSTERILANTS

THE production of sexual sterility in both sexes of an insect or other animal population by any method which does not adversely affect sexual behavior and mating competitiveness of the males and perhaps to a lesser extent females will exert greater effect in reducing the biotic potential of the population than can be achieved by killing or removing a like number of individuals of the population. This is a biological principle advanced by the writer in 1959. It should have great possibilities for meeting pest control or eradication problems. Research, however, has not yet advanced to a stage that it can be applied in practical operations.

But we are making progress. As the result of USDA research, several chemicals are now available which will induce complete and irreversible sterility in both males and females of a wide variety of insect species. For most insects, sterility can be achieved without serious adverse effects on the length of life and sexual vigor of the males. Chemicals that produce sterility in both sexes of insects are known as alkylating agents; they belong to the ethylene amine group.

If we can develop practical and safe ways to achieve sterility in insects as readily and as efficiently

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TABLE 2.—THEORETICAL EFFECT ON REPRODUCTION OF INSECT POPULATIONS SUBJECTED TO 3 TREATMENTS

Generation	No control (fivefold increase)	Control by killing (90 percent kill each generation)	Control by inducing sterility (90 percent sterility in both sexes each generation)
	Number	*Number*	*Number*
Parent.....	1,000	1,000	1,000
F_1.....	5,000	500	50
F_2.....	25,000	250	0
F_3.....	125,000	125	

as we can control them with insecticides, the impact on the reproductive potential of the population would be much greater than that produced by insecticides. The same relative effect should be possible for controlling or regulating vertebrate pests.

Theoretical Aspects

TABLE 2 shows the theoretical trend in a hypothetical insect population subjected to (1) no control, (2) control by killing, and (3) control by inducing sterility. We can assume, as for table 1, that the normal population in the absence of control efforts would increase fivefold each generation. Surviving insects not killed and those that mate successfully as fertile pairs would also result in a fivefold increase in population. We can further assume that the males sterilized are fully competitive with normal males in mating.

On the basis of the model, theoretical elimination would be achieved by treating two generations with a chemosterilant if 90 percent sterility of the population was achieved each generation. On the other hand, it would be necessary to treat at least eight generations to achieve theoretical elimination by applying insecticides, which would kill 90 percent of the insects each generation.

If a parent population of 1,000 insects were treated with a chemosterilant that produced sterility in 90 percent of the population, 900 of the insects could not reproduce by virtue of the direct effect of the sterility agent. This would be equivalent to killing, so far as reproduction is concerned. However, if the sterility does not adversely affect competitiveness of the males, each sterile male would have the same opportunity as a normal male to mate with the normal females. Since the sterile males, theoretically, outnumber the fertile males by ninefold, chance would provide for only 10 fertile matings. In the population treated with an insecticide, 900 would be killed but the remaining 100 could all mate successfully. Thus, the sterility method, theoretically, provides a bonus effect equivalent to the initial effect of the killing agent.

The relative degree of effect of a sterility agent versus a killing agent in population control depends on the level of kill or sterility achieved. In terms of the number reproducing successfully, a 50-percent sterility level is theoretically two times as effective as a 50-percent kill level. A 75-percent sterility level is four times as effective as a 75-percent kill level. A 90-percent sterility level is 10 times as effective as a 90-percent kill level. A 99-percent sterility level is 100 times as effective as a 99-percent kill level.

The bonus effect referred to is not the only potential advantage of the sterility method over the killing system. In comparing the two systems of popula-

tion control, we might say that the sterility principle has a four-dimensional effect, whereas the killing principle has only a single-dimensional effect.

When individuals in an animal population are killed, the only effect on the population is the elimination of those actually destroyed. When animals are sexually sterilized, without adversely affecting sexual competitiveness, the following effects are possible: (1) Those sterilized cannot reproduce—an effect equivalent to killing. (2) Sterile organisms compete with the fertile organisms and further reduce the reproductive potential of the population. This is the bonus effect already referred to. (3) The sterility method has a potential time effect.

In the model shown is table 2, the assumption is made that there are no carryover effects from one generation to the next with either the sterility agent or the killing agent. However, for insects or animals which live for long periods and overlap generations, the *time* effect is a *disadvantage* in population control when the killing system is employed, but is an *advantage* when the sterility system is employed.

In table 2, for example, if we assumed that one-half the parent population not killed survived and reproduced along with the F_1 progeny and if this happened each generation, the decline in the population would not be as great as indicated. On the other hand, for the population subjected to the chemosterilant treatment, if half of both the sterile insects and the fertile insects survived and overlap the subsequent generations, the effect on reproduction would be greater each generation by virtue of the survival of the sterile insects of the preceding parent population.

The *time* effect, theoretically, would be of major significance among vertebrate pests, which may survive for a number of years. For long-lived vertebrate pests, a 95-percent sterility level achieved only in a parent generation could theoretically result in complete elimination of the entire population in about 9 years. This is based on the assumption that one-half of the original population survived each year, and the normal successful reproduction rate for all reproducing pairs amounted to 2 reproducing progeny. In contrast, for a population subjected to a 95-percent kill, the population would theoretically return to the original level in about 9 years.

The fourth effect resulting from the sterility procedure is a *space* effect. In other words, animals made sterile have the ability to move and affect the reproductive capacity of the population throughout the range of dispersal. This could be a factor of vital importance for controlling both invertebrate and vertebrate pests.

Status of Research on Chemosterilants

A NUMBER of promising chemicals will produce sterility in insects. Original selections of materials for evaluation were made from compounds known to possess antitumor activity in animals. The Division's Pesticide Chemicals Research Branch, which has synthesized a number of other chemicals, is cooperating closely with the National Institutes of Health in the procurement of candidate chemosterilants. Those that are among the most effective are also among the chemicals that are promising as anticancer agents. Thus, the research on insect

sterilants and antitumor agents may be mutually complementary.

Little is known about the toxicological effects of the more promising chemisterilants. They are regarded as mutagenic in action and are also regarded as highly toxic to man and animals. Consequently, most of the research to date has been limited to laboratory investigations.

Laboratory experiments conducted by the Orlando laboratory with house flies in cages have, in general, supported the hypothetical effects of chemosterilants on insect population trends as depicted in table 2. Also, tests on small islands in Florida and around a Florida poultry farm have shown that fly populations can be effectively controlled with fly baits containing chemosterilants. Thus, the principle of insect control by this means has been established. However, in view of the lack of information on the hazards of chemosterilants to other organisms, every effort will be made to develop specific ways of exposing chemosterilants to insects in the natural environment.

Progress in the identification and synthesis of sex attractants that occur naturally in insects may be of vital importance in the potential use of chemosterilants. A high percentage of the males in an insect population may be attracted to highly active and specific sex attractants derived from females of the species. Perhaps it will be feasible in some cases to use the living virgin females of the species to lure males to a trap or to the female insect itself so that the males can be sterilized on contact with a chemosterilant. Success in controlling an insect by killing males may be very difficult, because the males of most or perhaps all insects are polygamous and a high percentage of kill may be required to achieve a high degree of reduction in reproduction. The sterilization of a high level of males could have a direct and proportionate effect on the reproductive potential of the females in the population.

The possibilities of using the natural population of pests for their own destruction through chemosterilants or other means cannot be fully appraised on the basis of current knowledge. But the practical development of this principle of pest control offers real opportunities for scientists of the future.

* * *

Goals For Pesticide Research

IN order to develop safer, more specific controls of pests, it is recommended that Government-sponsored programs continue to shift their emphasis from research on broad spectrum chemicals to provide more support for research on: (*a*) Selectively toxic chemicals, (*b*) nonpersistent chemicals, (*c*) selective methods of application, and (*d*) nonchemical control methods such as the use of attractants and the prevention of reproduction.

In the past few years, the Department of Agriculture has shifted its programs toward these specific controls. The Panel believes this trend should be continued and strengthened. Production of safer, more specific and less persistant pesticide chemicals is not an unreasonable goal; but its attainment will require extending research efforts beyond empirical approaches to more fundamental studies of subjects such as: The mode of action of pesticides; comparative toxicology; the metabolism of compounds in insects, plants, and higher animals; and the processes of chemical degradation and inactivation in nature. Such studies will also provide the information necessary to control those pests which are rapidly becoming resistant to currently available chemicals.

Only by stimulating training and basic investigation in the fields of toxicology and ecology are research needs likely to be met. An increased output of basic research data and a continuing supply of capable research personnel could be insured by a system of grants and contracts. Training grants, basic research grants, and contracts to universities and other nongovernmental research agencies funded by the Departments of Agriculture, Interior, and Health, Education, and Welfare would stimulate this research. In order to accelerate immediate progress, it might prove useful to explore the contributions which can be made by competent research people and their facilities in other countries.

From "The Use of Pesticides," a report from the President's Science Advisory Committee. May 1963. Washington, D.C.

OUTDOOR RECREATION RESEARCH

A Conference Report

THAT a unit of play is almost as important as a unit of work is distinctly a 20th-century concept of man. Under this concept, which was made possible by the phenomenal growth in technology and labor productivity, man naturally began to devote more and more of his time to activities other than that of earning his daily bread. And under this concept, it followed as a matter of course that man should see the need to study and analyze the resources concerned with this unit of play from the same vantage point as that established for the other unit. Thus, came the development of recreation research—more particularly outdoor recreation research, since the unit of play belongs predominantly in an outdoor environment.

Last year a group of national leaders in recreation sensed the urgency of taking a close look at the status of outdoor recreation research to see what might be done not only to stimulate the right kind of research, but also to devise ways of coordinating efforts. The outcome was the first National Conference on Outdoor Recreation Research, held at the University of Michigan in May 1963.

The impact of this conference is already being felt, and *Agricultural Science Review* believes that this relatively new area of research activity merits all the thoughtful planning and attention that can accrue from a wide understanding of the attendant needs and problems, especially those with which the disciplines in agricultural research are concerned. With that idea in mind, *Review* is including in this issue summary excerpts from a few of the formal conference papers and critiques. Space limitations, unfortunately, curtail the extent of our coverage. Complete proceedings are being published under the direction of the Conference Committee.

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NEEDED RESEARCH ON THE ECONOMIC AND POLITICAL SCIENCE ASPECTS OF OUTDOOR RECREATION

RALEIGH BARLOWE, Chairman
Department of Resource Development
Michigan State University

PUBLIC and private interest in outdoor recreation has definitely spiraled in recent years. This surge of interest has important roots in the past but, in many respects, can be viewed as a product of the growing affluence of our society.

Throughout much of our Nation's history, large segments of our population have held to a work ethic that has caused them to frown on widescale use of free time for recreation and play. Work has been exalted as a means to progress, and there has always been more work to do.

A shift away from this attitude has come about as we have approached the point at which we find it possible to provide virtually all of our citizenry with the requirements of a high level of life. Work is still held in high repute, but it has also become a means to play. Recreation has gradually come into its own. We have found it desirable to substitute additional leisure for the production we could secure from more hours of labor. Workers now enjoy a shorter workweek, higher real incomes, and greater mobility than in the past. People are subject to educational and advertising influences that nurture a desire for outdoor recreation; expenditures of time and money for this purpose have become an expected aspect of modern life.

This changing situation has freed recreation from numerous shackles that have contained it in the past. Far from remaining the province of children, the nobility, and the wealthy, recreation has become the privilege of every man. One could say that it has emerged from the recesses of man's aspirations, from his hopes for the good life. It has become a new opportunity for the masses, a big business for many operators, a major challenge for administrators and public leaders, and a problem of political consequence for the Nation as a whole.

Our major economic and political problems with outdoor recreation can be boiled down to five significant areas: (1) Measurement of the demand for outdoor recreation, (2) supplying opportunities for outdoor recreation, (3) securing political and financial support for proposed developments, (4) investment and benefit-cost considerations, and (5) public and private responsibilities in the provision of opportunities for outdoor recreation.

Measurement of Demand

STUDIES of present tastes and preferences can help guide us in our recreation programs. Consideration, however, should also be given to prospective changes in these tastes. Most of us have had enough contact with the out of doors to feel that significant areas of open space should be reserved and developed for future enjoyment. Future generations may or may not share this feeling. It has been suggested that man's appreciation of the amenities of Nature may be bred out of him through centuries of urban living. This end result is hard to imagine, but changes there will be, if for no other reason than that future generations will grow up in a far more crowded world than that we have known.

Supplying Opportunities

MUCH of the research on the supply and demand aspects of outdoor recreation should be interrelated. Research showing that major concentrations of new demand can be expected in and around our larger cities, for example, should be linked to studies designed to augment the supplies of facilities to be provided at these sites. It must be recognized also that less land and fewer facilities will be developed for outdoor recreation than many of us would like. Research can help provide guidelines for optimum development and use of the areas and facilities that are provided.

Securing Support

ADEQUATE sources of financing must be found if we are to face up to our challenge in the public outdoor recreation field. There is little doubt that an affluent society such as ours can afford the needed developments. Important decisions must be made, however, in the initiation, timing, and financing of these developments. Accomplishment of our overall goal calls for education and farsighted leadership, and also for research that can help point the way to securing the necessary political and financial backing for new recreation programs.

Investment and Benefit-Cost Considerations

INTEREST in the business and investment side of recreation is heartening to the recreation enthusiast. Stern questions may be asked, however, about the economic soundness of some of our current interests. Analyses are needed of the extent to which unneeded farmlands can profitably shift to recreational uses, of the income potential that farm vacations and leased hunting or fishing privileges offer in different areas, and of the actual extent to which emphasis on outdoor recreation may help solve the problem of low incomes in agriculture.

Similar research emphasis should be given to the extent to which recreation developments can be

used to stimulate local economies. Will developments that are subject to highly seasonal use actually pay out? Can they stimulate local economies enough to promote genuine economic growth? If not, can they be used effectively to stem economic lag or decline? Going a step farther, research can indicate whether public funds can be better used to stimulate economic development and growth with other types of ventures than recreation and if greater returns per dollar of investment can be secured in prosperous areas than in the so-called "distressed areas."

Public and Private Responsibilities

IT is quite obvious in the United States that public agencies cannot be expected to provide all the increase in opportunities that will be needed. Developments in the private sphere are needed and should be actively encouraged.

From a research point of view, the problem of public and private responsibilities can be divided into three sub areas: Public use of public developments, public access and use of privately owned lands and developments, and private use of private properties. Each of these subareas provides a number of economic and political problems worthy of research consideration.

Research has already shown us that we have a tremendous problem ahead in providing opportunities for outdoor recreation for a growing population. Research will provide many of the answers to problems that will unfold as we face up to the challenges ahead. It should be apparent from the start, however, that this is no problem for public agencies alone. The public and private spheres of the economy both have responsibilities for the provision of additional opportunities for outdoor recreation. Greater coordination is needed between the activities of various governmental agencies and between the programs of these agencies and private operators. Public assistance to private operators is needed in many instances to help them operate effectively alongside the public agencies in meeting the problems ahead.

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OUTDOOR RECREATION RESEARCH IN FEDERAL AGENCIES

V. L. HARPER, Deputy Chief
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THERE is no need to reiterate the familiar statistics on today's recreation impacts, nor to discuss at length the effect of these impacts on Federal programs. It should be sufficient to say the Federal agencies have taken major steps along several avenues to help meet some of the impacts of outdoor recreation and its changes in our American scene.

In 1956, the National Park Service embarked upon its Mission 66; the Forest Service started Operation Outdoors in 1957; TVA, the Corps of Engineers, and the Bureau of Reclamation have expanded and stepped up their programs to provide more water-based recreation; and Congress authorized and created the Outdoor Recreation Resources Review Commission in 1958. The Commission report early in 1962 sparked the establishment of the new Bureau of Outdoor Recreation.

In 1961, Congress authorized the Housing and Home Finance Agency to provide financial assistance to local governments to purchase and preserve open space in urban areas; and last year's Food and Agriculture Act authorized Federal assistance to finance and stimulate the conversion of a substantial area of farmland to recreation use.

I believe outdoor recreation research at its present level is not sufficient, considering the nature of the problems involved and considering the very rapid growth of this activity both currently and prospectively. I base this conclusion, not on any precise measurement of the need for research, but rather on general criteria. One measure is that agncies, both public and private, are asking critical questions for which there are no satisfactory answers as yet, and, at the present level of research effort, there will be no satisfactory answers in any reasonable length of time.

Another measure is that the investment going into research relative to that spent in action programs is quite small. The ORRRC reports tell us that current annual expenditures by Federal agencies for outdoor recreation action programs are about $200 million. The total annual outlay by Federal agencies for outdoor recreation research is probably less than $500,000, which means it is less

than three-tenths of 1 percent of the cost of the action programs. Judged by standards which apply to some other rapidly growing fields of activity, it seems obvious to me that outdoor recreation research should be greatly strengthened.

But how fast and how much this acceleration will be and the direction the research will take will depend upon many factors. To a large extent it will depend upon how well the problems needing research attention are identified and the urgency that will be felt for the knowledge research will produce.

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OUTDOOR RECREATION RESEARCH: SOME CONCEPTS AND SUGGESTED AREAS OF STUDY

MARION CLAWSON and JACK L. KNETSCH
Resources for the Future

AS we contemplate the certain increased demand for outdoor recreation in the United States over the decades ahead, and as we review the scope and content of research in outdoor recreation, some conclusions and suggestions about outdoor recreation research for the next decade or two seem to present themselves clearly.

Research on the important problems of outdoor recreation will be more important in the future than in the past. The problems will be more difficult, and the intuitive approach, under which a man leans heavily on his own experience generalized to a broader situation, simply will not be adequate.

But usable results from research will flow rather slowly; no miracles can be expected tomorrow. Research workers must develop improved and adequate methodology, test it rigorously under a variety of conditions, and then accumulate a body of research results. Premature reliance on untested research might well bring the whole concept of research into disrepute; for the next few years, we shall have to continue to rely heavily on the intuitive approach which we think inadequate for the longer run.

The most important immediate task of research is conceptualizing. We need more useful, more sophisticated, more imaginative analytical models into which to fit data and by which to analyze difficult problems. Until we have them, more data may be as confusing as helpful. Analytical models must be tested adequately and under a variety of conditions; there is no place in this field of intensely practical problems for theorizing which cannot be or is not put into research application.

Once better analytical models are developed and tested, there is a major need to collect data on a much larger scale, and to analyze it as fully as possible. We need to know the purpose for which we collect data, before we spend scarce money and manpower resources on its collection. Replication or multiplication of research studies of the same or similar kinds will help build up a body of research findings that will both test the universality of the research techniques and will provide sounder guides to planning, administration, and financing.

The need exists for several research organizations more or less specializing in recreation research. If the field is to be developed rapidly, then it needs the push which can best come from organizations whose major interest and concern is recreation research. The Bureau of Outdoor Recreation can serve this function, among others; perhaps other organizations with a specialized interest in outdoor recreation research can be developed.

But much research on outdoor recreation probably—and we would say, properly also—will be done by various specialists in research organizations with interests other than outdoor recreation. We have in mind the Forest Service, forestry schools, land-grant colleges, and others. It will be carried out by foresters, wildlife management specialists, park specialists, economists, sociologists, political scientists, and others of various professional backgrounds. We think that, as a general rule, it is better to have this research undertaken by men thoroughly competent in their basic field, who learn about outdoor recreation as they progress in research, rather than to attempt to develop "recreation researchers" who then would learn about economics, political science, forestry, or whatnot. Men with various professional backgrounds should be encouraged to seek research projects on problems in outdoor recreation. One function of the specialized recreation research agencies will be to bring such problems to the attention of these specialists.

The need definitely exists for a better clearinghouse of recreation research. The fragmentation and diversification of the field of recreation research, obvious to anyone who explores it even casually, means that men who work in one part are often unaware of men who work in another part—even those at their institution or in their State. We do

not attempt to spell out how the clearinghouse function can best be performed, but we think the need is real.

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A CRITIQUE: SOME NEEDED RESEARCH IN RECREATION RESOURCE DEVELOPMENT

HUGH B. MASTERS
Director, Georgia Center for Continuing Education, University of Georgia

I BELIEVE that one of the most needed subjects for research in the field of outdoor recreation is that of human behavior. I think we must find ways of protecting the out of doors from people, just as our technologists and manufacturers are now concerned with developing ways of protecting people from the out of doors. At the same time, however, I believe we must find new ways of enabling people to make greater use of the out of doors and thus derive greater enjoyment, or re-creation, from it. I believe people, most pepole, can and want to be taught new ways of using and appreciating the nautral resources, whether it be a new way of using a fishing rod or a new way of appreciating the beauty of a mountain.

The Georgia Center has just completed preliminary studies of the feasibility of establishing in northeast Georgia an outdoor recreation research experiment station. We conceive of this station as being similar to the very successful agricultural experiment stations, in that we would conduct experiments and demonstrations, the results of which would be made available to all those working in the field.

I don't wish to dwell overmuch on the proposed outdoor recreation research experiment station with which I am personally involved, but it does represent an approach to all of these research problems we have been concerned with at this meeting. This station intends, if it is established as we conceive it, to address itself to finding as many answers as possible to these questions. We hope to maintain instructors to teach new skills to our partcipants, to maintain or contract with professional researchers to formulate and implement programs of research into many and varied phases of outdoor recreation, including human behavior, financing of recreation facilities, proper use of private land for recreational opportunities, training of professional recreationists, and changes in "classic" types of recreational pursuits.

I see no reason why similar endeavors should not be carried out in other regions of the country; in fact, I hope, and shall attempt to help to see, that they shall be. We have by no means solved all the problems attendant to establishing our own station, but the idea, I am firmly convinced, is sound and will eventually be consummated.

The ORRRC report, to which the Georgia Center had the privilege of contributing a study report, said that, "Perhaps no other activity involving so many people and so basic a part of our life has received less attention from qualified investigators and scientists." I think such criticism as this, and the self-criticism we are providing ourselves with here, is healthy, although the situation to which it refers is not. Yet I believe the situation is changing rapidly for the better, and that well-conducted research by qualified investigators will soon be given its proper place in the growing field of outdoor recreation.

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EDUCATION IN OUTDOOR RECREATION

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THE outdoor recreation boom, like any new social phenomena, presents special challenges to colleges and universities. It is, in large measure, in our centers of higher education where we must look for leadership if we are to tackle new social problems fundamentally and on a broad front. This is true in meeting research needs as well as in strengthening educational preparation for the jobs that outdoor recreation requires. In fact, at the colleges and universities, research and education feed one another.

It may be more important to avoid the danger of premature professionalism of the field, than to meet every demand for qualified workers. Before rushing into the breach with rosters of new courses, hand-tailored curricula, and new and impressive degrees, we need to ask ourselves two basic questions.

First, what are the jobs that are needed to deal with outdoor recreation in the years ahead; and to what extent do they require special kinds of training or new combinations of special training?

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Second, to what extent does this training require a body of knowledge that must be developed and transmitted through an intellectual process, rather than be acquired through job experience or apprenticeship types of training?

I suggest that there are four components of outdoor recreation which have special relevance to the question of university training. These are: (1) Directing or supervising recreation activities; (2) managing the natural resources dedicated to recreation; (3) allocating additional resource areas for recreation use; and (4) forecasting the demand for outdoor recreation. These are identifiable functions, each of which presumably requires some body of concepts, methods, and skills.

Directing Recreation Activities

THE function of directing recreation activities dominates in activity-oriented areas such as playgrounds, playfields, and city parks. This function, however, may become increasingly important in resource-oriented areas at points of visitor concentrations. In activity-oriented areas, the professional recreation worker must, first of all, be a teacher. Regardless of his philosophic motivation in teaching people to re-create, his success depends primarily upon his ability to organize and supervise people in the pursuit of those activities which make up recreation. His job may demand a wide range of performance, from teaching activity-skills in a way that the participant finds a satisfying experience, to conceiving and integrating recreation programs in a way that the community will support them as an essential part of its pattern of living.

Managing Resources for Recreation

A UNIQUE characteristic of outdoor recreation is the intimate relationship between the consumer and the recreation site. Unless the consumer is managed as an element of the ecosystem, he may impair or destroy the production facility in the process of consuming the recreation service it provides. Here I believe we must recognize the emergence of quite a new type of resources management problem. It is a problem that poses research challenges and may suggest the need for training programs that bring together new combinations of concepts, methodologies, and skills of the highest professional order.

A recreation resources manager would be something more than a wildlands manager. Presumably he would possess equal competence in all the technical areas involved in managing a resource area for recreation. Consequently, his training should seek to give him competence in four fields: (1) the ecology of the area, with skill in adjusting use to environmental potentials and limitations; (2) the psychology and preference of users, with skill in directing their use to harmonize demands and capacity of the area to serve; (3) site design, with skill in planning new developments; and (4) administration, with skill in financial management, personnel, and decisionmaking.

Although we can make a pretty good case for a person trained as I have described, there is a real question whether such training is now possible. Until we have some further specific research on user-site interdependencies, we have little to teach except that derived from experience of those who have held such a job and have met the hordes as well as the payroll. There is a further question as to whether we can expect to cram into one man the breadth and depth of training that the function calls for. Answers to these questions may become clear only with time.

Allocating Resources for New Recreation Areas

A MAJOR aspect of the lively public interest in outdoor recreation stems from a concern about the amount and kind of land and water that are available for recreation uses.

It is no doubt true that more often than not in the formulation of regional resource plans, outdoor recreation has not received the consideration that it deserves. Lands for recreation and open space must now be considered as one of the major structural components of a regional development plan, in the same manner as transportation networks and natural drainage systems. If they are to serve that role, we must strive for regional recreation plans that are formulated with full recognition of competing land-use demands, and properly integrated with highway and water development plans. This means, it seems to me, that regional recreation planning requires something more than a recreation specialist. In my judgment a recreation specialization can better be acquired by any well-trained regional planner.

From the perspective of the training program,

the need is to inject a greater degree of recreation consciousness into the training in regional resource development and planning. This may suggest the desirability of courses or seminars covering such things as recreation demand patterns and behavior, and considerations of resource potentials and limitations. This kind of educational experience would give to the otherwise undifferentiated regional planner some special acquaintance with outdoor recreation problems. However, the central training core must continue to be regional development planning.

Forecasting Outdoor Recreation Demand

IMPROVEMENTS in demand forecasts depend upon a wide range of basic understandings about the role of recreation in society. These understandings will come not from specialized understandings about recreation, but rather from deeper understandings about society.

The important point is that the performance requirements are those of the researcher, and the competences required are those of the behavioral sciences. The unity is greater in the structure of the disciplines than in the structure of recreation. A more thorough analysis and forecasting of recreation demand calls for research by psychologists, sociologists, and economists. Here the central emphasis should be to encourage well-trained social scientists to tackle those aspects of the recreation problem requiring their particular competences. The fruits of their research should provide firmer bases for directing recreation activities, for managing recreation resources, and for regional recreation planning.

* * *

Corporate Organization on the Farm

AS might be expected, the trend toward fewer and larger farms, higher investments, and greater production efficiency is exerting no small influence on the scope of research by agricultural economists. Within this framework of study, corporate-type organization of the family farm is being more closely analyzed. One of the most recent of these studies was conducted by E. D. Chastain, Jr., and W. F. Woods of the Alabama Agricultural Experiment Station, Auburn University.

These researchers wanted to determine if incorporation is a threat to the existence of family farms or if it offers a way for family farms to continue to thrive under changing economic conditions.

From case studies in Alabama, they concluded that corporate-type management may have much to offer individual family farms. It is not, however, the solution to present maladjustments in American agriculture. Moreover, the authors say, corporate farming does not signify the end of the traditional family farm. These conclusions were published in the Alabama Station's Bulletin 343, "Adaptability of Corporate Organization to Family Farms."

Insofar as the stability of the family farm is concerned, these Alabama findings parallel those recently announced by USDA's Economic Research Service. Agricultural economist, Radoje Nikolitch, states that three main characteristics highlight the structure of American agriculture: (1) The large number of small farms with relatively little production is fast decreasing. (2) The small number of big farms with a considerable amount of production is increasing. (3) The great bulk of agricultural products comes from farms on which the operator and his family do most of the work.

In 1944, 94.5 percent of all farms were so-called family farms; they accounted for 66.5 percent of all farm marketings. In 1959, these family businesses accounted for 95.7 percent of all farms and for 70 percent of all farm marketings.

The Nation's biggest farms—those with $40,000 or more in sales—totaled 102,000 in 1959. Significantly, 40 percent of these were family farms; they accounted for one-fourth of all marketing by this size group.

What is the trend in corporate-type farm organization in the United States as a whole? Although the exact number of incorporated farms is not known, it is estimated to be approximately 14,000, most of which are operated by families. The real picture—not only on the extent of incorporation, but also with respect to its fundamental attributes and its contribution potential to American agriculture—should be forthcoming after a new research study by Economic Research Service is completed next year.

BODY SIZE AND METABOLIC RATE IN THE DOMESTIC FOWL

William J. Mellen

Basal metabolism may be defined as the minimal energy expended by an animal in the fasting and resting state, and in a thermally neutral environment, for the maintenance of respiration, circulation, body temperature, glandular activity, and other metabolic functions. The basal metabolic rate can be measured directly as the rate at which heat is given off, but is most frequently determined as rate of oxygen consumption. Generally, heat production increases with surface area, but surface area is difficult to determine accurately; therefore, most researchers working on this problem have resorted to using a function of body weight, which can be determined more accurately.

Metabolic rate of animals is affected by type of food, by exercise, age, environmental temperature, and disease. Thus, much of the current research on the nutrition, physiology, genetics, and ecology of the domestic fowl involves in vivo *oxygen consumption or energy metabolism determinations.*

In this article Dr. Mellen presents his views on certain phases of this field of knowledge—many of which have been controversial since the time of Lavoisier.

SEVERAL times in the past few years I have been more than a little disturbed when reading research papers in which the authors presented data on metabolic rates in the domestic fowl. Basically, I am fond of such data, for I have personally done hundreds of metabolic rate (MR) determinations on chickens and have bravely contributed many of the results to the literature. The source of my concern is this:

Too many investigators either have been unaware of or have chosen to ignore the well-established dependency of weight-specific MR on body size. This negligence has led to numerous errors, discrepancies, ambiguities, and misinterpretations in the literature.

Before elaborating on this statement and offering personal opinions for remedial action, I would like to develop a background for discussion by a selective review of the literature on MR and body size. First, a quotation from von Bertalanffy (*4*): [1]

> "The relation between metabolic rate and body size belongs to the classical topics of physiology. It goes back over more than a hundred years to the time when Sarrus and Rameaux, Bergmann and Leuckhart, and Richet noticed that weight-specific metabolic rate, that is, the intensity of metabolism as measured by oxygen consumption or calorie production per kilogram of body weight, decreases with increasing body size."

It is also true, and generally recognized, that MR *increases* with increasing body size if expressed in terms of oxygen consumption or heat production *per animal.* Usefulness of this relationship in statistical control of the effect of body size on MR will be illustrated later.

It is standard practice to express human MR's in terms of body surface area (Cal./sq. m./hr. or day).

[1] Italic numbers in parentheses refer to "Literature Cited," p. 49.

This indicates that workers in human metabolism and clinical medicine are still happy with Rubner's famous surface law, despite the vigorous contention by Benedict that deviations from this "law" are both numerous and large.

Rubner believed that basal heat production is proportional to the surface area of the body, and is about the same per unit of surface area regardless of the size of the animal. Much of the controversy over his surface law has revolved around the question of causality: Does heat loss from the body surface determine the heat production? Or, is the body size-surface area-MR relationship merely a coincidence? Brody (*5*) believed that the neuroendocrine system exclusively governs heat production and that surface area has no causal significance. Burton (*6*) concluded that: "Which of these two characteristics, the metabolism or the properties of heat transfer, is the controlling factor and which is the controlled, seems to be a question for philosophy rather than for physiology." Kleiber's (*16, 17*) consideration of six major theories which have been advanced to explain the Surface Law has led him to conclude that only two of the six are valid: (*a*) that relating MR to rate of heat transfer between animal and environment, and (*b*) that relating MR to blood circulation.

A practical difficulty arises from the fact that there is no good definition of the *effective* surface area of any particular type of animal. Furthermore, actual determination of the surface area would be tedious, if not impossible.

Krogh proposed in 1916 that the relationship between size and metabolism would be clarified if heat production were expressed as a function of weight (W) to some power (n). He provisionally suggested that n be 2/3, since surface area varies with the 2/3 power of weight in geometrically similar bodies of the same density. More recent proponents of using W^n are Kleiber (*16*) and Brody (*5*), who have advanced telling arguments in its favor.

Brody (*5*) crystallized his viewpoint as follows: "It is theoretically more logical and practically simpler to relate metabolism, not to surface area or to $W^{2/3}$, or to 'active mass,' or 'protoplasmic mass,' but to the noncommital *physiologically effective* body size represented symbolically by W^b, the value of the exponent b to be determined from actual data." At various times Brody derived values for b—most of them about 0.7—from his own and others' data. One does this by finding the value of b in the parabolic equation, $Y=aX^b$, which is represented by a straight line when "per animal" oxygen consumption or heat production (Y) is plotted against body weight (X) on log-log graph paper. The slope of the line is b, calculated by the usual methods ($b_{yx}=Sxy/Sx^2$) after changing the regression equation to the form, $\log Y=\log a+b \log X$.

In a review article, Kleiber (*16*) stated: "Our recent analysis favors again the 3/4 power of body weight as the metabolic unit of body size." Kleiber's $W^{3/4}$ was based on an interspecific relationship of body size and metabolism in animals ranging in weight from 0.15 kg. to 680 kg., and had not been shown to apply intraspecifically. However, he suggested that it be used in studies within a species unless proved to be inappropriate.

Some authors have warned against the routine and indiscriminate use of any given power of body weight in MR studies. For example, Winchester (*34*) found that "use of a power function of body weight to express relative body size within the species studied" was subject to limitations. He reported that heat production in hens varied with different powers of body weight during different months. Brody (*5*) presented evidence to show that, during growth, metabolic rate referred to W^b is not as uniform as it is among mature animals, and gave the

following reasons: (1) There may be a "work-energy cost" of growth not separable from "basal metabolic cost." (2) Early life is essentially poikilothermic (coldblooded). (3) The neuroendocrine mechanism in thermoregulatory control does not attain maximal function until late in life. One must admire Brody's recommendation that the value of b in W^b should be determined from data at hand.

Modern Poultry Literature

THE preceding historical review is by no means exhaustive. But it clearly shows that the problem of expressing MR's in relation to some unit of body size, particularly in comparing animals of different sizes, has been recognized and studied for a long time. One would hardly expect, then, to find contemporary investigators presenting their MR data as "volume of oxygen consumed (or Calories produced) per unit weight per unit time" without some attempt to adjust for body weight differences—or at least a statement justifying the lack of such adjustment! I recognize that if there are no appreciable weight differences, adjustment is unnecessary. In other cases, appropriate adjustment may not alter the experimenter's conclusions, although I suspect that it would improve the sensitivity and precision of most MR experiments. But I am most concerned about the apparent lack of recognition that the problem even exists, as indicated by most of the reports now to be reviewed.

Perek and Sulman (*26*) determined basal metabolic rate (BMR) in eight Leghorn hens before, during, and after molting, and reported that it was 400–500 cc. O_2/kg./hr. during egg-laying and 600–700 cc. O_2/kg./hr. during molt. Since these authors did not compare body weights for the laying periods versus the molting period, a critical reader would wonder to what extent this large increase in MR was due to loss in body weight during the molt. Lest some may think I am straining a little here, let me give an example of how important weight changes in hens can be in modifying their MR's:

Dukes (*8*) presented BMR data for mature White Plymouth Rock hens from November 1931 through February 1932. Eleven birds did not lay during this time, at least two separate determinations were made for them at intervals of at least 1 month. Since changes in body weight and MR in these 11 hens were not complicated by changes in size and activity of the reproductive system, they furnish a good example for illustrating my point. I have averaged the least and greatest weights for these birds (in all except one there was an increase from the first measurement to the later one) and the associated weight-specific MR's, with the following results: At their smallest mean weight, 2.33 kg., the mean MR was 2.34 Cal./kg./hr. At the largest mean weight of 2.73 kg., the mean MR was 2.04 Cal./kg./hr. Thus for a mean weight change of 0.40 kg. (0.9 lb.), there was an associated change in MR of 0.30 Cal./kg./hr. This amounts to a 13-percent or 15-percent change in MR, depending on which value is used as the base for the calculation.

In a study of the effects of thiouracil on semen quality in the fowl, Shaffner and Andrews (*28*) obtained data on resting metabolism in mature Barred Plymouth Rock males. Figure 1 in their paper seems to indicate a continuous decline in MR over a 16-week period in birds fed thiouracil, while control MR remained essentially constant. However, again the picture is cloudy, because the MR's were expressed as cc. O_2/kg./hr. and "the males receiving thiouracil gained significantly more than the controls" during the experiment. Was all or part of the decline in weight-specific MR due to the greater body size of the treated birds? This question cannot be answered from the information published. Because the males had been fasted "at least 12 hours" before oxygen consumption was measured, and because of the later discovery that the metabolism-depressing effect of ingested thiouracil disappears between 12 and 24 hours following withdrawal of the drug (Mellen (*19*)), the authors' conclusion with respect to MR is open to question.

Criticism similar to that in the preceding paragraph can be directed at the report of McCartney and Shaffner (*18*) on effects of thiouracil and thyroprotein (iodinated casein, "Protamone") in laying pullets. These workers used their data on fasting metabolism (cc. O_2/kg./hr.) to support the statement that mild hypo- and hyperthyroidism had been induced, but also pointed out that "the females receiving thiouracil gained more than the controls, while the females receiving thyroprotein weighed slightly less at the end of this period than they did at the beginning." Again the effects of body weight are confounded with those of treatments, and whether or not this confounding was important cannot be estimated from the published data.

Another paper reporting metabolic effects of feeding thiouracil and thyroprotein to chickens is that by Singh and Shaffner (*29*). Chicks were used rather than mature birds, but again the MR data were presented as ml. O_2/kg./hr. with no correction for differences in body weight among groups.

More confusion has been contributed to the literature by the report of Huston et al. (*13*) on oxygen consumption in adult fowls of three breeds held at different environmental temperatures. MR data are given as ml. O_2/lb./hr., and no body weights are furnished, although weights of similar birds are given in a companion paper (Huston and Carmon (*12*)). Table 1 of Huston et al. (*13*) reveals an apparent anomaly in the sex differences in MR. Mean MR's for New Hampshire and White Rock males are higher than those for the females of those breeds, both in birds held at a constant high temperature and in those kept since hatching at uncontrolled temperatures. In White Leghorns, however, MR was higher in the females, which would be expected on the basis of their smaller size. This situation resulted in a highly significant breed X sex interaction in the data analysis.

But how does one interpret this interaction? Is the true MR of New Hampshire and White Rock roosters (but *not* of White Leghorn males) so much higher than that of hens that the difference shows up even when the males are "penalized" for their greater size by the expression, "ml. O_2/lb./hr."? Actually there is some evidence in the older literature [2] for a higher BMR in mature males than in mature females of heavy breeds; but the point to be made in our present discussion is that the failure of Huston et al. to correct their MR values for differences in body weight, or at least to provide weight data, has resulted in a presentation which is difficult to interpret.

Even more to the point for present purposes is the conclusion drawn by Huston et al. concerning breed comparisons in MR. With no apparent recognition that the large differences in size between the heavy breeds and the Leghorns must have influenced the weight-specific MR's reported, they state: "Oxygen consumption of the White Leghorn was significantly higher than [that of] New Hampshires and White Plymouth Rocks." They then use this conclusion to support their belief that the Leghorn has a higher thyroid activity than the heavy breeds; and further state in the companion paper (Huston and Carmon (*12*)) that the well-known superior heat-resistance of White Leghorns "may, in part, be due to a relatively higher thyroid activity."

Huston, Edwards, and Williams (*14*) have reported oxygen consumption data on twenty 12-week-old White Rock males—10 grown at 88° F. and 10 grown at 66° F. Mean body weights were 2,070 grams and 2,368 grams, respectively; and the corresponding oxygen values ("O_2/hr," no volume units given) were 1,778 and 1,977. Apparently these figures represent ml./bird/hr.; therefore it is not surprising that the larger birds showed the larger oxygen uptake. As we might expect, this paper contains the statement that oxygen consumption was higher in birds held at 66° than in those held at 88°.

Using the data on body weight and oxygen consumption given by Huston, Edwards, and Williams (*14*), I have calculated the MR's as ml. O_2/lb./hr., and find that, to be consistent with the previous report by Huston, Cotton, and Carmon, they should have stated that the oxygen consumption of birds

[2] I have restudied, and in some cases recalculated, BMR data for mature or nearly mature heavy-breed birds reported by Mitchell and Haines (*24*), Mitchell et al. (*23*), and Kibler and Brody (*15*). When the MR's are expressed as Cal./kg./hr., male and female values are essentially equal in each of the three studies. Since all the males were considerably larger, this indicates that their MR's were actually greater than those of the females. This conclusion is borne out, in the paper cited, by BMR's expressed as Cal./sq.m./day. I have not been able to find comparable data for White Leghorns.

grown at the lower temperature (379 ml./lb./hr.) was slightly lower than or no different from that in the other group (390 ml./lb./hr.). Obviously, neither system used by Huston and coworkers for expressing MR was satisfactory.

The recent report by Washburn et al. (*33*) furnishes a somewhat different example of a penalty incurred by failure to correct MR data for body size differences. In their research, mean oxygen consumption was 570 ml./kg./hr. in thiouracil-fed chickens and 890 ml./kg./hr. in controls. Body weights were not given, but I have learned from Washburn that the thiouracil-treated birds were significantly smaller than their controls. This being so, I cannot disagree with the conclusion that MR was significantly lower in the treated groups, even after 12 hours of fasting (12 hours with no thiouracil intake); but would point out that either appropriate adjustment of the MR figures, or expressing MR in terms of W^b (Brody (*5*)), would have yielded an even more striking comparison.

For example: Using mean weights furnished by Washburn, and converting them to $kg.^{3/4}$, I find that the mean MR's in his control and thiouracil-fed lots were approximately 935 and 565 ml. $O_2/kg.^{.75}/hr.$, respectively.

A more serious problem arises in a subsequent publication by Washburn and Siegel (*32*), in which MR's (l. O_2/kg./hr.) at 68 days of age are compared in two lines of White Rocks, one selected for high and one for low 8-week weights. The weight difference between these lines was highly significant from 1–140 days of age; therefore, the system used for expressing MR was a poor choice. The mean values of 760 ml./kg./hr. for the high-weight line and 700 ml./kg./hr. for the low-weight line were not significantly different; but to me they indicate the possibility of a real difference, for reasons which already have been amply discussed. Proper treatment of these data might lead to a reversal of the conclusion that there was no line difference in MR.

A recent paper by Thornton (*31*) furnishes an example of an experiment in which no adjustment for size differences was necessary. Oxygen consumption and body temperature were measured simultaneously in hens while the metabolism chamber was immersed in water. Temperature of the water bath was gradually increased from 60° F. to 100° F. over a period of about 1 hour. Oxygen uptake (ml./kg./hr.) was recorded at the initial, the lowest, and the highest body temperature for each bird, and the MR's corresponding to the low- and high-temperature points were expressed as percent of the initial MR and percent of the low-temperature MR, respectively. Since the critical comparisons made were between MR readings taken on the same bird within a period of 1 hour, there would have been no advantage in using surface area, $W^{3/4}$, or some other device to minimize effects of body size on MR.

In addition to my own modest contributions, there are at least two other papers in the recent poultry literature in which the MR-body size problem is acknowledged. Morrison et al. (*25*) compared basal heat production (estimated by indirect calorimetry) in chicks fed antibiotics and in controls, and reported body weight, absolute oxygen consumption, absolute heat production, and heat production per unit weight to the ¾ power. It's a bit ironic that in this example of meticulous and complete presentation of data, referring metabolism to metabolic body size ($W^{3/4}$) did not help in interpretation of the data, because there were no weight differences between treated and control groups. Baldini (*1*) is another investigator who has been concerned over the influence of body size on MR. He attempted, in one experiment out of five, to avoid this influence by choosing birds from each of his two treatment groups on the basis of body weight. This procedure has obvious limitations.

Recommendations

HE who publicly criticizes the efforts of his peers, even though motivated by noble purpose, incurs an obligation to offer constructive suggestions. The ones I am about to make are based on several years of personal experience and cogitation, but can undoubtedly be improved upon by others who, hopefully, may be stimulated by this paper.

My first awareness of the importance of the MR-body size problem in certain types of work dawned during the early stages of my thesis research at Cornell University, just 12 years ago. Since birds in various treatment groups usually varied considerably in mean weight, it seemed apparent that use of weight-specific MR (metabolism per unit weight per unit time) would be inappropriate. It was equally obvious that using total oxygen consumption per bird unit time would be a mistake. I was

considering other possibilities, such as use of Kleiber's $W^{3/4}$, when a friend made a unique suggestion based on his keen interest in and prediliction for statistics and biometry. Steven C. King, my officemate and fellow graduate student at the time, proposed that statistical control of the effect of body size on MR could be realized by adjusting mean MR's, expressed as volume of O_2/bird/hr., for the average within-lot linear regression of oxygen uptake on body weight. (I see no reason why this technique could not also be used when the MR values are expressed on a "per unit weight" basis, but this involves the additional operation of dividing each "per animal" MR by the appropriate body weight.) In effect, this means that individual MR's (Y) and corresponding body weights (X) are used in covariance analysis to test significance of mean differences in MR. The mean within-lot regression coefficient (b_{yx}) is used to adjust the mean MR ($\overline{Y}$) for each treatment lot according to the difference between its mean weight ($\overline{X}$) and the overall mean weight ($\overline{\overline{X}}$):

$$\overline{Y}_a = \overline{Y} - b_{yx}\ (\overline{X} - \overline{\overline{X}})$$

The rationale for this type of statistical control is discussed by Snedecor (*30*) in his chapters on linear regression and covariance, and by Cochran and Cox (*7*, ch. 3), among others. Examples of application of this approach in MR studies with chickens have been reported by Mellen (*19*), Mellen and Hill (*20, 21*), and Mellen et al. (*22*). I am not aware that anyone else has used covariance in MR experiments, but strictly analogous applications have been employed by Hoffman et al. (*11*) for minimizing effect of body weight on gland weights in comparing several strains of chickens, and by Fox and Bohren (*10*) for adjusting feed efficiency data for differences in body weight among four breeds of fowl. All of these are examples of a departure from the standard use of covariance, in which it is known or assumed that the treatments do not affect the X values. In the studies cited in this paragraph, the authors have taken advantage of the fact that treatments *did* affect X (body weight) as well as Y (MR, gland weight, feed efficiency). Snedecor (*30*, p. 407) gives a similar example based on a fertilizer study, and says, "Since treatment obviously affected X, there is no hope of estimating Y *free from the effects of* X; both X and Y are affected by the fertilizer. What may be done is to learn if there is any effect of fertilizer on Y over and above that contributed through X."

Naturally there are precautions to be observed in the use of covariance in MR experiments. In the first place, covariance analysis is based on the same assumptions underlying the analysis of variance—". . . that treatment and environmental effects are additive, and that the experimental errors are independently distributed in the normal distribution, with a common variance" (Cochran and Cox, *7*, p. 83). In addition, we must consider the characteristics of the regression being used to make the desired corrections or adjustments. It is not strictly valid to adjust each $\overline{Y}$ by use of the average b_{yx} unless it can be shown that the various within-group regressions do not differ significantly. Where the within-group regressions do differ significantly, adjustments should be made by means of the individual regressions rather than the pooled regression. This problem was recognized and discussed by Hoffman et al. (*11*) and by Fox and Bohren (*10*). In MR-body size relationships, we have the further complication that the true regression is usually curvilinear (Brody, *5*; Kleiber, *16*). However, over the range of body weights in most experiments, the slight departure from linearity can be ignored without affecting the results appreciably.

Although I recommend the covariance approach, and believe it to be applicable to many MR studies, there are experiments in which it may be difficult or impossible to apply. For example, one may be dealing with so few animals that he has little confidence in the estimate of the mean b_{yx} or in a test of whether or not the various within-lot regressions are the same. In such cases, it may be better to attack the problem differently, such as by relating MR to the ¾ power of weight. Figure 1 (p. 26) illustrates one case in which this device served quite well to eliminate the influence of body size on MR (compare the bottom set of regression lines with the other two sets). I expect that approximately the same picture would have been obtained with other powers of weight in the range of 0.7–0.8.

If one has ample data for making a reliable estimate of the true MR-body size relationship in a given experiment, and if there is some good reason for using W^b rather than a regression correction, it would be well to calculate the value of b for the specific data at hand, as recommended by Brody (*5*).

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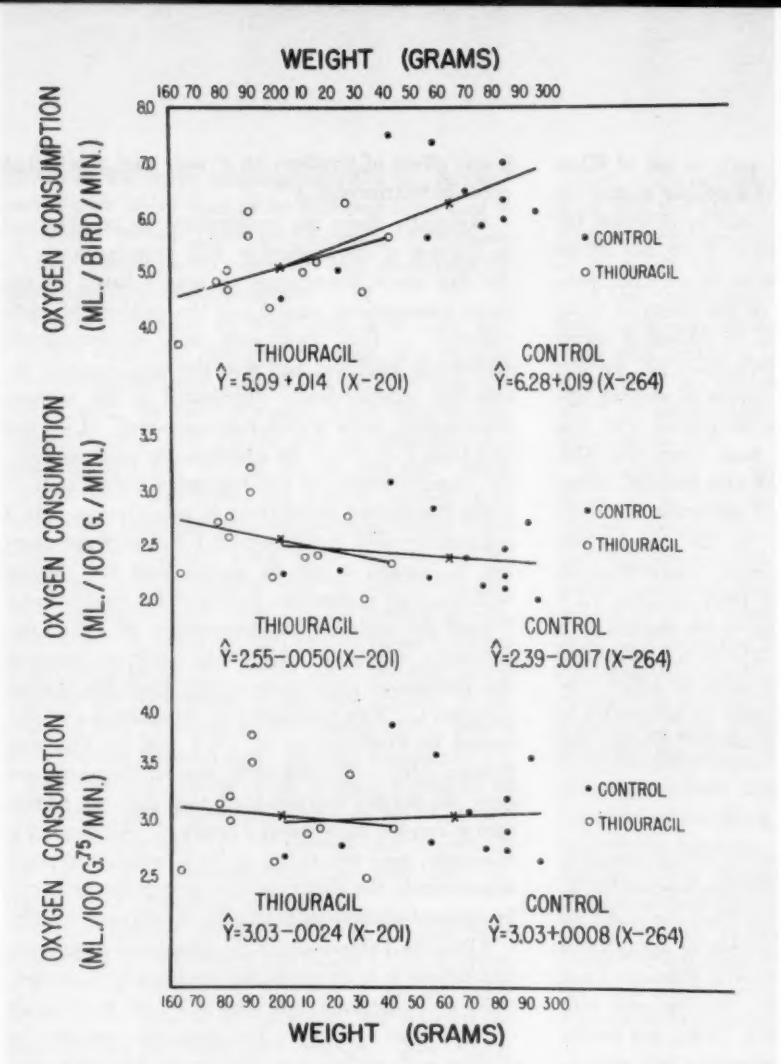


FIGURE 1.—Relationships between body size and metabolic rate when the same data are used in three different ways. Based on duplicate determinations of oxygen uptake in White Leghorn chicks after 12–20 hours of fasting—12 controls and 12 thiouracil fed. (From Mellen, *19*.)

A few words of caution are in order regarding very young chicks, because there is evidence that the relationship between metabolism and body weight may change significantly during the first week or two of life. Data of Barott and Pringle (*2*) show that MR expressed as ml. O_2/gram/hr. was actually higher in 2-week-old chicks than when they had been smaller (2–6 days of age)—but only at or near the critical temperature, i.e. the environmental temperature below which the MR of a resting, fasting animal must increase if body temperature is to remain constant (Dukes *9*, p. 631). Romijn (*27*) reported that heat production per unit weight in North Holland Blue chicks *increased* with increasing size up to 3 weeks of age (150 grams), then steadily decreased thereafter. More recently, Beattie and Freeman (*3*) showed that oxygen uptake per unit weight increased with increasing growth, in chicks from two sources, up to an average weight of 60–70 grams. "Respiratory intensity" continued to increase, though less sharply, up to 100-gram weight in group A; but it *decreased* slightly in group B as the birds increased in weight from 70 to 100 grams. There was also an indication, in group B only, of a change in slope of the line showing the relationship of oxygen consumption *per bird* to body weight—again at a weight of about 70 grams.

My final and major recommendation is this: Regardless of what approach may prove best in research involving the MR–body size problem, let's at least realize that there *is* something to be concerned about, and try to do something about it. This problem has been ignored by many people, but it has refused to go away.

(Continued on p. 49)

Selective Breeding and the Production of

NEW FOREST TREE VARIETIES

Jonathan W. Wright

SELECTIVE breeding—now a major item of interest among tree breeders—received serious attention only after provenance testing, species hybridization, and species introduction were already underway.

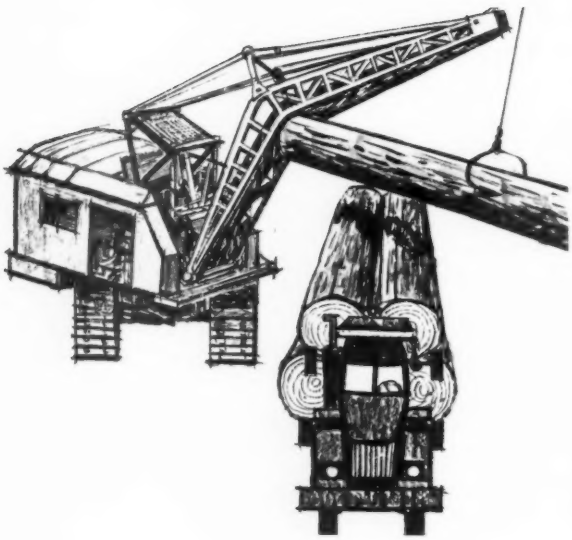
As defined in this paper, selective breeding includes selecting and crossing of superior individuals within a race or within two similar races, determining inheritance patterns in the resulting progenies, and devising ways of mass producing the progenies. In contrast with provenance testing or species hybridization, trees and their progenies are considered invidiually rather than as average members of large populations.

Selection programs generally depend for success on the presence of additive genetic variance, with a linear relationship between genotype and phenotype. Other types of variation may be present but cannot be incorporated into true-breeding varieties without more elaborate experimentation than is practicable now.

Serious work on individual-tree inheritance dates from the 1930's; intensive work from the later 1950's. There are now hundreds of separate projects. Despite the inherent difficulties of genetic work with a long-lived organism, enough sound evidence has accumulated to show that selective breeding can result in appreciable genetic improvement of economically important traits. Other reasons for the current popularity of such studies are the universal availability of parental material, the supposed theoretical simplicity of the approach, and the rather widespread feeling that selection of superior trees is the only practical approach to tree improvement.

Selective breeding is much more complex than the mere selection of "plus" trees in the forest; and other approaches, such as provenance testing, are at times advisable.

The centers of greatest activity have been northern Europe and southeastern United States, where studies have been initiated on the inheritance of form, growth rate, wood density, and oleoresin content of the most important conifers. There are less extensive programs in Australia, the Union of South Africa, and parts of northern United States. Relatively little has been done on individual-tree inheritance in hardwoods or tropical species.



SELECTIVE BREEDING APPROACHES

OF the various approaches to selective breeding, progeny testing seems to offer the surest results and is generally supplanting the less intensive methods involving only mass selection. The question of whether the progeny tests should be with open-pollinated or control-pollinated seed has to be resolved for each individual case in view of heritability, cost, and urgency of the need for improvement.

Phenotypic Selection of Parents

BINGHAM and Squillace's work can be cited as an example of successful parental selection (*3*).[1] In the late 1940's and early 1950's they searched in northern Idaho and western Montana for the rare canker-free trees of western white pine (*Pinus monticola* Dougl.) in stands nearly decimated by blister rust. Ease of climbing, accessibility, and heaviness of fruiting were also considered in making the selections, which were to be control pollinated at an early date. Several factors made the probability of success greater than it would be for most traits or most species. The trait being selected was of major economic importance; many cooperators assisted in finding the desired trees. The bimodal frequency distribution of cankering (0 per tree in selections, scores to hundreds per tree in others) and clonal tests in a related species provided strong advance evidence for the presence of genetic variability. Some "plus" trees could be spotted from a considerable distance as green against a background of dead or dying trees.

Zobel's selection work for high wood density in loblolly pine(*P. taeda L.*) presented more complex problems (*10, 13, 18*). An increment core had to be extracted and weighed for every sampled tree. It was not practicable to make all the selections in stands of the same age or same growing conditions. At the outset there was little information on the relation between density and environment. Hence, supplementary studies had to be undertaken before "plus" trees could be recognized.

Clonal Tests

IN the late 1930's, Riker of Wisconsin selected 163 blister-rust-free parents from heavily cankered eastern white pine (*P. strobus L.*) (cited in *16*). He grafted the selections on seedling rootstocks, and grew the grafts and seedling controls in a replicated test at Wisconsin Rapids. *Ribes* plants were interplanted to promote heavy infection. After 20 years, nearly all trees of 40 clones were living, whereas most of the remaining clones and seedling controls were dead. A supplemental open-pollinated progeny test showed statistically significant differences among progenies, but did not show a general superiority of the offspring of selected parents. Thus, the clonal test provided good evidence on the total genetic variance but none on the ability of parents to transmit resistance by seed.

Schütt conducted a 2-year greenhouse test with artificial inoculation of Scotch pine (*P. sylvestris L.*) clones selected for phenotypic resistance to a needle cast fungus (cited in *16*). Clones from resistant ortets averaged 22 percent diseased; those from susceptible ortets, 82 percent.

There are numerous poplar (*Populus*) clonal tests. Most were made for testing species hybrids or ecotypes and therefore do not apply to selective breeding as here defined.

[1] Italic numbers in parentheses refer to "Literature Cited," p. 37.

Clonal Seed Orchards

PLANTATIONS Nos. 4 to 6 of the Swedish Institute for Forest Tree Breeding and Genetics furnish an example of a clonal seed orchard (*1*). Forty-five Scotch pine trees were carefully selected from an area of a few hundred square miles for their phenotypic excellence in stem form and branch size.

From each selection enough grafts were made during 1957–60 to supply 237 living grafts per clone. The resulting grafts were planted on a 13- by 13-foot spacing at three places near Umea, about 50 miles outside the zone of collection; the three plantings total 17 hectares (42 acres). Clones were thoroughly mixed to promote cross-pollination. Thinning, if done, will be on the basis of clonal performance. Quantity seed production is expected by 1965 or 1970.

A different type of clonal seed orchard, containing 100 ramets from each of 13 parental-generation clones, was recently established with western white pine at Sandpoint, Idaho. The clones were selected on the basis of their proven ability (in an earlier F_1 progeny test) to produce superior progeny. The grafts were made in the late 1950's and by 1970 are expected to produce commercial quantities of F_1 seed with an average 30-percent (compared to 5 percent for controls) resistance to blister rust. Meanwhile, superior F_1 seedlings are being progeny tested in an F_2 planting that will be evaluated about 1970. At that time the F_1 clones with superior combining ability will be grafted in another orchard which will produce F_2 seed about 1980. It is estimated from the F_1 intraclass correlation that average resistance in the F_2 will be 50 percent. Thus, F_2 seed, when available in quantity, will supersede F_1 seed from the 1960 orchard.

Orchards of the Swedish type are most common. They cover an area of 537 hectares (1,323 acres) in Sweden and areas almost as large in Finland, Denmark, Germany, and southeastern United States (*10, 12, 13, 16*). There are plans to convert a small percentage to the north Idaho type by establishing F_1 progeny tests that will permit thinning on the basis of progeny performance.

Seed Production Areas

IN American terminology, a seed production area is a high-quality stand, usually natural, which is heavily thinned to increase seed production. The usual objective is to lower seed production costs or to assure a continued supply of average-quality seed. Selection pressures are relatively low and genetic consequences are similar to those following intensive silviculture.

A 5-year-old open-pollinated progeny test of loblolly pine in Texas furnishes one of the few genetic evaluations of a seed production area (*13*). Evidently the thinning did not result in genetic improvement because the best performance was from commercial seed. The comparative growth rates are shown below.

TABLE 1

TYPE OF PARENT	PROGENY	
	HEIGHT	D.B.H.[1]
	Feet	*Inches*
Selected parents from seed production area (seed collected before thinning)	15.4	3.0
Average parents from nearby stand	15.1	3.0
Mostly poor phenotypes used for commercial seed collection	16.3	3.3

[1] Diameter at breast height.

Development of Inbred Lines

A SMALL amount of selfing has been attempted in about 30 species of trees (*16*). Severe inbreeding depression or self-sterility occurred in 80 percent of the experiments. Prevalence of floral mechanisms adapted to outcrossing supports the limited selfing data in indicating that natural inbreeding is rare. Presumably, breeding systems based on outcrossing will be most useful in temperate-zone forest trees. Avoidance of inbreeding requires that selection and progeny testing be done on a large scale.

Some thought has been given to use of the maize approach—the development of inbred lines to be outcrossed at a later date. No serious attempt has been made to start such a program, and practical difficulties would be great. Growing of a useful number of selfed progenies would involve years of concentrated breeding effort and maintenance of special weed-free plantations. Also, many dwarf conifers (not necessarily selfs) have not fruited in 40 years.

Bulk Progeny Tests

A BULK progeny is one containing offspring of many different trees within a species. Numerous examples are provided by provenance tests in which each progeny represents a stand. Bulk progenies could be used in a selective breeding program. They would provide a simple means of determining heritability of single traits and the quality of seed produced by a seed production area or clonal orchard.

Half-Sib or One-Parent Progeny Tests

A HALF-SIB progeny test results when each progeny (=half-sib family) includes the half-sib offspring of a single seed-parent. Most such tests start with open-pollinated seed; the only large exception is a slash pine (*Pinus elliottii* Engelm. var. *elliottii*) study in northern Florida.

A large half-sib progeny test can also function as a seed orchard. It is cheaper and often better than a clonal orchard (*5, 16*). Moreover, a large test may be started in a single season. Measurement of the seedling progenies provides inheritance data from which to compute actual gain for the first generation and projected gain for later generations. The inheritance data also permit the practice of family selection, which is much more efficient than phenotypic selection for traits of low to medium heritability.

A Scotch pine study started in Michigan in 1960 illustrates a one-parent progeny test (*17*). Included in it are open-pollinated offspring of 100 old trees located in 5 East German stands. After being studied in a 4-replicated nursery test, the seedlings were transferred to 5 permanent plantings, each containing 5 to 10 replicates. A 4-tree-per-plot design with an 8- by 8-foot spacing was used. A few trees flowered in the second to fourth years, and general fruiting is expected by age 8.

The following generalizations can be made from the 3-year nursery measurements and parental data. (*a*) Large and statistically significant genetic improvements could be made from family selection for growth rate, needle length, needle color, time of first-year bud formation, or time of secondary needle formation. (*b*) Parent-progeny correlations were too low to justify parental selection. (*c*) Lack of discernible genetic correlation between traits indicates that selection should be for one or two traits only. (*d*) The ratio of between-stand to within-stand genetic variance varied by trait. In some, stand selection gives the most gain; in others, family selection.

If the East German ecotype were known to be best for Michigan, the Michigan experiment could also be considered as a seed orchard. This would start with removal of all trees of poor progenies about 1968. The thinning would continue until only the best 10 trees in the best 5 progenies remained after age 30. Also, about 1968 an F_2 progeny test would be started by using the best individuals in the best F_1 families as parents. By 1976 the F_2 test should supersede the F_1 test as a seed orchard.

In southern Sweden there is a 50-year-old one-parent progeny test of Norway spruce (*Picea abies* (L.) Karst) and a few 12- or 13-year-old tests of Norway spruce and Scotch pine. For each planting the parents were selected from similar sites over an area of a few hundred square miles (*9*). In one of the two Scotch pine plantings there was a significant positive correlation (r=0.56) between mother tree height/diameter ratio and progeny height at age 10, and a significant negative correlation (r=−0.43) between mother-tree volume and

progeny height. In two of the four spruce plantings there were significant positive correlations (r= 0.49, r=0.35) between mother-tree height/diameter ratio and progeny height at age 12. The remainder of the parent-progeny correlations were not significant.

Approximately 100 acres of one-parent progeny tests of loblolly pine have been established recently in southeastern United States (*10*). Most follow a randomized complete block design with 25-tree plots and 4 replicates. Their primary purpose is to provide information on family performance to guide the thinning of already-established clonal orchards.

Black wattle (*Acacia mearnsii* De Wild.) is grown in the Union of South Africa for tannin contained in the bark. A series of open-pollinated progeny tests were established for its improvement (*8*). Two have been evaluated, giving 5-year and 11-year data, respectively. Significant between-family differences show that selection based on family performance resulted in a genetic reduction of 12 percent in gummosis damage and in gentic gains of 5, 9, and 5 percent in diameter, bark thickness, and percent tannin content, respectively. Total tannin yield was 40 percent greater in the best than in the average families. Except in percent tannin content, parent-progeny correlations were too low to justify parental selection as an improvement method.

Two 11-year-old one-parent progeny tests of Norway spruce in southern Norway showed that the care used in selecting the parental phenotypes was justified (*11*). The progenies of most of the 83 selected parents were taller than were 5 bulk progenies from average trees in the same regions.

Full-Sib or Two-Parent Progeny Tests

A FULL-SIB progeny test results when each progeny (= full-sib family) includes the full-sib offspring of a particular tree × tree combination resulting from controlled pollination. A large full-sib test can function as a seed orchard. It can also show the gain which would result from any other type of orchard.

As compared with a half-sib test, a full-sib test provides more information per parent but information about fewer parents. If production of 100 control-pollinated progenies is a possibility, as would be the case for young pines and spruces, full-sib tests are advisable. On the other hand, half-sib tests are more practical if controlled pollinations are very time consuming, as would be the case on very large trees or on most oaks and maples. It is often desirable to start with an F_1 half-sib test and to progress to full-sib tests in later generations.

The oldest large two-parent progeny tested was started by Bingham and Squillace in northern Idaho (*3*). They crossed 18 blister-rust-free western white pines in various combinations in 1950 and harvested seed from 61 matings (90+ good seed per mating) in 1951. The seed was sown in 1952 and the seedlings were placed in a permanent, 9-replicated 10-tree-per-plot outplanting in 1954. Evaluation for rust resistance consisted of a survival count in 1957. Survivals were as follows:

TABLE 2

TYPE OF POLLINATION	TYPE OF PARENT	SURVIVAL
		Percent
Open	Unselected	5
Do	All selected	9
Controlled	....do	18
Open	Parents No. 17, 21, 25, 58 [1]	15
Controlled	Parents No. 17, 21, 25, 58 crossed among themselves	32
Do	Parents No. 17, 19, 22, 58 [2] crossed with various selections.	27
Do	Parents No. 17, 19, 22, 58 crossed among themselves	35

[1] These had highest general combining ability in the 1-parent test.
[2] These had highest general combining ability in the 2-parent test.

DATE AND TYPE OF SEED ORCHARD	GAIN IN RUST RESISTANCE
	Percent
1950, all 18 clones	11
1960, 4 clones shown best by 1-parent test	23
1960, 4 clones shown best by 2-parent test	26
1950 1-parent test thinned to 4 best families	7
1950 2-parent test thinned to 6 combinations among the 4 best parents	20
1960 F_2 2-parent test starting with seed from the 4 best families in F_1 1-parent test and thinned to 6 combinations among 4 best parents	27
1960 F_2 2-parent test starting with seed from the 6 best F_1 full-sib families and thinned to 6 combinations among 4 best F_1 parents	40

TABLE 3

The realized *broad-sense* family heritability of rust resistance in the Idaho study was 0.87; the realized *narrow-sense* family heritability was 0.67. From those estimates the genetic gains from various types of seed orchard can be calculated as above.

Comparison of these estimates indicates that improvement in blister rust resistance will be greatest—

per generation if clonal orchards follow progeny tests;

per decade if two-parent progeny tests are used as seed orchards;

per unit of effort if one-parent progeny tests are used as seed orchards.

The 2-parent progeny testing of western white pine continued in autumn 1960 with the sowing of 28 progenies (7 females × 4 males) (*7*). At age 1, between-family differences attributable to male parent were 14 and 27 percent of the mean height and epicotyl length, respectively. Corresponding percents attributable to female parent were 14 and 22 percent, respectively.

The first of many contemplated loblolly pine two-parent tests was started in 1963 as part of the North Carolina State-industry improvement program (10). One planting included 16 progenies; the other 50. It is planned to cross each selected female with four "tester" males and to replicate.

REALIZED HERITABILITY AND ESTIMATES OF GENETIC GAIN

The results of the various types of experiments can be summarized best in terms of realized heritability which measures the amount of "reach" actually attained. "Realized" rather than "true" heritabilities are used because they can be calculated from existing forest tree experiments. Also, they can be applied without correction factors if used for the same population and selection method from which they were derived.

Heritabilities are of interest because of the relation:

Genetic gain = Heritability × Selection differential

This should be a total or broad-sense heritability if applied to clones; an additive or narrow-sense heritability if applied to seedlings.

Realized total heritability (RH_T) can be estimated from clonal tests by one of the following formulas.

(1) RH_T = intraclass correlation = $\frac{V_C}{V_C + V_e}$ (applicable to plot means)

(1a) $RH_T = \frac{V_C}{V_C + V_e/r}$ (applicable to clone means)

where

V_C and V_e are variances between and within clones, respectively

r=number of replicates

(2) $RH_T = \frac{\text{Genetic gain}}{\text{Selection differential}} = b$=regression of ramets on ortets

Realized additive heritability (RH_A) must be estimated from progeny tests by one of the following formulas. The tests must be replicated to use formulas 3, 3a, or 5, but need not be when using formulas 4 or 6. The forms given are the proper ones when plot means are used in the analysis of variance.

(3) RH_A=intraclass correlation=$\frac{V_{hs}}{V_{hs}+V_e}$ (applicable to plot means)

(3a) $RH_A = \frac{V_{hs}}{V_{hs}+V_e/r}$ (applicable to progeny means)

This can be simplified to

(3a) $RH_A = \frac{F-1}{F}$ (applicable to progeny means)

(4) $RH_A = \frac{\text{Genetic gain}}{\text{Selection differential}} = b$=regression of half-sib progenies on parents

$=\frac{1}{2}$ "true" heritability (narrow-sense)

(5) $RH_A = \frac{V_F+V_M}{V_F+V_M+V_{FM}+V_e/r}$ (applicable to full-sib family means)

(6) $RH_A = \frac{\text{Genetic gain}}{\text{Selection differential}} = b$=regression of full-sib progenies on mid-parent means

="true" heritability (narrow-sense)

where

V_{hs}=Between-half-sib progeny variance

V_F, V_M, and V_{FM}=Variances due to female, male, and female-male interaction, respectively, from a replicated full-sib progeny test

V_e=Error or within-progeny variance

r=number of replicates

$F = \frac{\text{Between-progeny mean square}}{\text{Within-progeny mean square}}$

TEST	REALIZED HERITABILITY
Wood specific gravity:	
Formula No. 1	0.64.
Formula No. 2	0.00 (comparison between 5-year-old ramets and ortets).
Formula No. 2	0.30 (comparison between mature ortets and 5-year-old ramets).
Formula No. 3	0.94.
Formula No. 4	0.15 (correlation coefficient was 0.84 with 13 d. f.).
Height: Formula No. 4	0.00 (correlation not significant).
Diameter: Formula No. 4	0.00 (correlation not significant).

TABLE 4

Formulas 1, 1a, 3, 3a, and 5 show the amount of genetic variation among plots in a replicated clonal or progeny test. The estimates must be used with selection differentials based upon differences among plots, clones, or families. For example, if the best seedlings are 100 centimeters taller than average and the best progeny is 10 centimeters taller than average, 10 centimeters is the proper selection differential for use with a heritability derived from formula 3a or 5.

The following examples show the variation in realized heritabilities according to method of calculation and population.

Van Buijtenen studied heritabilities of three traits in a Texas population of loblolly pine (*15*). For wood specific gravity, his experimental material consisted of a 5-year-old, 6-clone test; and a 6-year-old, 15-progeny half-sib test. For height and diameter his experimental material consisted of a 5-year-old, 29-progeny half-sib test. The estimates are given in Table 4 above.

Goggans measured several wood characters in two 8-year-old half-sib progeny tests of loblolly pine (*5*). Offspring of six Louisiana parents were represented in one test; of eight Georgia parents in the other. The tracheid determinations were made from wood from a single (1959) ring. The heritabilities are given in Table 5, which shows how the story may change from one trait to another and from one stand to another.

Zobel and coworkers also studied wood specific gravity and tracheid length. Their experimental material was a 3-year-old, 38-clone planting of Georgia and South Carolina slash pine (*Pinus elliotti* Engelm var. elliotti (*18*). For the two traits, respectively, realized total heritabilities were 0.48 and 0.56 (formula 1); 0 and 0 (formula 2).

Wright measured several growth characters in a series of 3-year-old half-sib progeny tests of Scotch pine (*17*). The series included 20 families from each of 5 German stands and 10 from each of 3 Belgian stands. The family heritabilities (calculated by formula 3a) of four traits in the five German stands are shown in Table 6. Note that in some traits the heritability varies considerably from stand to stand. This is to be expected because it is very easy to obtain a sample of 20 parents with much more or much less genetic variability than would be considered typical of an extensive population.

Family heritabilities were also calculated for the entire German or Belgian samples. This was done by formula 3a after estimating variance from the pooled between-family-within-stand mean squares. The heritabilities thus determined apply to relatively large areas in which there is assumed to be no between-stand variation. The heritabilities would be increased if the rather large amount of between-stand variation had also been included. For the entire German or Belgian samples the realized heritabilities were 0.82 and 0.80, respectively, for height, 0.68 and 0.73 for autumnal color; 0.81 and 0.82 for date of first-year bud formation; 0.68 and 0.75 for secondary leaf presence; 0.55 and 0.51 for leaf length.

Bingham et al. worked with a 5-year-old, 18-par-

TABLE 5

TRAIT	REALIZED HERITABILITY DERIVED FROM *Formula 3a* — Louisiana sample	*Formula 3a* — Georgia sample	*Formula 4* — Georgia sample
Specific gravity	0.76	0.87	.....
Percent summerwood	.86	.92	.....
Summerwood tracheids:			
Wall thickness	.84	[1] .00	0.09
Radial lumen diameter	.44	.31	.01
Radial width	.81	[1] .00	.06
Tangential width	.59	.27	.26
Springwood tracheids:			
Wall thickness	.13	[1] .00	.13
Radial lumen diameter	.59	.68	.14
Radial width	.76	.65	.14
Tangential width	.80	.49	.29

[1] Between-family differences were not significant. The heritability is effectively but not mathematically zero.

TABLE 6

TRAIT	REALIZED FAMILY HERITABILITY IN GERMAN STAND NUMBER *1*	*2*	*3*	*4*	*5*
Height, age 2	0.77	0.83	0.74	0.70	0.81
Winter foliage color, age 2	.71	.67	.68	[1].00	.83
Bud formation date, age 1	.67	.76	.88	.84	.81
Leaf length, age 2	[1].00	.77	[1].00	.47	[1].00

[1] Between-family differences were not significant. Heritability is effectively but not mathematically zero.

TABLE 7

TRAIT	REALIZED HERITABILITY CALCULATED BY FORMULA (3)	(3a)	(4)
Diameter	0.30	0.83	0.20
Bark thickness	.25	.68	.24
Percent tannin content	.....	.75	.62
Gummosis, percent attack	.....	.76	.....

ent, 61-family half-sib and full-sib progeny test of western white pine (*3*). Realized additive heritabilities of blister rust resistance were 0.03 (formula 4), 0.69 (formula 5), and 0.13 (formula 6). Also, a total family heritability of 0.87 was calculated from a variant of formula 5.

In California a 15-year-old half-sib progeny test of ponderosa pine (*Pinus ponderosa* Dougl.) included offspring from several elevational zones. The family heritability was 0.39 (formula 3) or 0.57 (formula 3a) (cited in *16*).

Heritabilities were calculated from Moffett and Nixon's data on black wattle trees by three different formulas (*8*). The estimates were similar for the 5- and 11-year experiments if calculated for both. The more complete set from the 5-year experiment is presented in Table 7 (p. 35).

Toda, working with *Cryptomeria japonica,* D. Don used a very different approach (*14*). There is a limited number of older one-clone plantings in Japan from which estimates of environmental variance may be derived. There are many seedling plantations from which total variance can be calculated. Genetic variance, used to calculate total heritability, was obtained by subtracting the environmental from the total variance. The method entails rather involved corrections for age of planting and site variability pattern.

Among the similarities in heritabilities is the general lowness of estimates based on parent-progeny or ortet-ramet relationships. Also noticeable is the relatively large number of high (0.8+) family heritabilities based on formulas 3a and 5. As a consequence, it can be inferred that family selection is usually much more productive than phenotypic selection.

REDUCING THE LONG TEST ROTATION

BREEDERS prefer to make their selections as early as possible and yet be sure that they maintain superiority at maturity. Data applicable to the problem are scarce. From species and provenance trials there are several correlations between performance at ages 2 or 3 and at ages 15 or 20. However, it is doubtful if they should be applied when breeding within ecotypes.

Ruden (*11*), working with open-pollinated progenies of Norway spruce, found a good (unstated) correlation between height at age 4 and height at age 11. About 80 percent of his seedlots maintained the same relative rank—above or below average—at both ages.

Nilsson summarized data from a 50-year-old, 36-progeny, 1-parent progeny test of Norway spruce conducted in Sweden (*9*). Of the 5 progenies which were tallest at maturity, 2, 2, 4, and 4 had been among the five tallest at ages 6, 8, 10, and 20, respectively. Sixty-nine percent of the progenies were above average at ages 6 and 50 or below average at the same 2 times; the corresponding percent at ages 8, 10, and 20 were 69, 86, and 89, respectively. Apparently, juvenile selection at age 10 would be almost as good as mature selection. With correlations as high as these, devoting of the 50-year test period to a five-generation breeding program would have resulted in appreciably more gain than could have been accomplished in one 50-year generation or in two and one-half 20-year generations.

Undoubtedly, following the same progenies throughout progeny-life is the best way of learning the earliest time at which selection is reliable. But this is time consuming and data are needed now. Indirect approaches can provide some information. The presence, but not the absence of strong relations between juvenile and mature progenies can be indicated by significant, positive correlations between mature parents and juvenile progeny. Zobel, following ontogenetic relations within the parental generation, concluded that several aspects of loblolly pine wood quality were best assessed after age 10 (*10, 13*). Bengston followed exceptionally tall and average 1-year-old seedlings of slash pine for 8 years (*2*). The select group maintained its initial superiority, although the relative amount of the superiority decreased. Others have also followed "super" seedlings for 8 to 10 years; most found that the initial group advantage is maintained or increased.

MUTATION INDUCTION AND SELECTIVE BREEDING

IONIZING radiation produces gross chromosomal changes such as deletions, inversions, and translocations. So do some chemicals. These chromosomal changes are detectable cytologically and usually result in growth abnormalities (shortened internodes, albinos, etc.) of little commercial value.

Ionizing radiation also produces gene mutations. The majority are recessive and have small effects.

Radiation could be a useful tree breeding tool if enough of these small mutations could be incorporated into a new variety. A few new varieties of crop plants have come into being in this manner. In each case it was necessary to start with material of known genetic composition, treat a few thousand seeds, discard the plants with visible defects, and progeny test the remainder through enough generations to fix the desired traits. The mutation process itself was a random one and the direction of improvement was a function of selection among the thousands of progenies.

In the past decade there has been limited work with X-rayed tree seed. As with other organisms, gross abnormalities have been the main result. It seems probable that large-scale, continued progeny testing would also have to be used with trees if useful new varieties were to result.

Recent breakthroughs in theoretical genetics make directed mutation in micro-organisms a reality. Will they eliminate the need for the traditional approaches outlined in this paper? If so, I would guess that the earliest date would be two or three tree generations from now. Before this could happen, several things must be known about the trees: Ways of altering the base sequence in the DNA molecule (known now only for viruses and bacteria), inventory of present proteins and their effects on growth, effects of a substituted protein on growth, gene locations at which substitutions are to be made (i.e., a chromosome map normally requiring several generations of progeny testing), and ways of incorporating single substitutions into millions of trees (i.e., inheritance patterns). So it would seem that the traditional approach needs to be intensified before it can be superseded.

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REVOLUTION IN WEED SCIENCE

W. C. Shaw and A. J. Loustalot

WEEDS and their control are as old as history. They were there in the Garden of Eden with Adam and Eve, but though the principals were banished, the aliens remained and are with us today. The revolution began early. The aliens arrived in this country along with Captain John Smith and his little band of colonists in 1607. Documents of the first colony showed that weeds were among the most serious obstacles to producing the necessary food and fiber to sustain the colony. Indeed there is much evidence that weeds played a vitally significant role in the failure of the colony at Jamestown.

Science accepted the weed challenge and has turned it into a revolution which has evolved through a succession of human energy, the energy of man and livestock, mechanical devices from the sickle to the diesel tractor with tillage implements of all kinds. But always there was the hoe. So strong was this image that the man with the hoe has always occupied an important place in agriculture.

But as science and technology combined, the use of chemical energy for weed control has opened new horizons for increased efficiency in the production of food, fiber, and livestock in American agriculture. A new discipline has evolved—weed science.

To understand this revolution and to analyze its impact on agriculture, it is necessary to understand the ecological significance of weeds and their control.

Native vegetation in most geographical areas in the United States was originally not very efficient or economical as a source of food for livestock and humans. As the human and livestock populations increased, it has been necessary to replace the native vegetation with more productive, more efficient, and more economical plants for food and fiber.

The sequence of events that occurs in plant successions when native vegetation is disturbed or cultivated fields are abandoned is well known. Weeds comprise an early stage of plant successions that terminate with the climax-vegetation characteristic of the area. This is one of the fundamentals of plant ecology.

In our efforts to produce economic crops, we attempt to utilize fully all available scientific technology to balance the vegetation at a highly produc-

tive level. Weed control is a basic, essential, and important aspect of this fundamental ecological process. Weeds compete with crops for water, light, and mineral nutrients. Weeds increase the cost of labor and equipment, reduce the quantity and quality of crops, and harbor insects and diseases. Thus, weed control in crops is basically an ecological problem.

LOSSES CAUSED BY WEEDS

ALTHOUGH much progress has been made in improving weed control methods, the weed problem still represents a major challenge to optimum efficiency in farming operations. The annual national loss in agricultural production due to weeds and the cost of weed control, estimated to exceed $4 billion, are among the most serious problems facing the agricultural economy. Weeds cause damage in many ways, including the following:

In Productivity . . . Yields of crops and livestock are reduced or impaired by failure to control weeds. In many instances the presence of particular weeds in fields determines the choice of crops to be planted. Weeds tend to reduce the value of agricultural land. They increase production and harvesting costs, impede production mechanization, and reduce efficiency of equipment and other operations. Excessive tillage to control weeds frequently causes damages to the crops and soil. Aside from the loss in production of forage, brush on rangelands increases the cost of handling livestock and prevents efficient management.

In Quality . . . Weeds in crop products such as the lint of cotton, and hay, and in leafy and other vegetable crops reduce their quality. In addition, weeds such as wild onion, wild garlic, and bitterweed impart off-flavors to milk and frequently the inferior product cannot be sold. The presence of burs in wool is one of the greatest losses suffered by the wool industry. Noxious weed seed contamination greatly reduces crop seed value and sometimes prevents its sale. Weeds and weed debris in grains and other farm products reduce their sales value or cause spoilage in storage. Certain serious contaminants, such as crotalaria seed in corn or soybeans, dodder in alfalfa or clovers, and wild vetch in cereals, necessitate costly cleaning operations prior to marketing.

In Efficiency of Water Management . . . Aquatic weeds reduce markedly the flow of water in irrigation and drainage canals. Obstruction to flow causes high water levels in canals and streams that result in flooding, seepage into adjoining areas or poor drainage, breaks in canal banks, and inadequate delivery of irrigation water to farms located at a distance from the water source. In addition, reduced velocity of flow causes increased siltation, reduced carrying capacity, and necessitates more frequent mechanical cleaning. Aquatic weeds that break loose and weeds of the floating type obstruct weirs, gates, and other structures. Also algae and fragments of plant material clog sprinkler irrigation system equipment. Aquatic weeds promote breeding grounds for obnoxious insects such as mosquitoes. They reduce recreational values by interfering with fishing, swimming, boating, hunting, and navigation of otherwise navigable streams. The decaying organic matter produced by aquatic weeds causes off-flavors in potable waters. Weeds on watershed areas and flood plains utilize large amounts of water and thereby deny its use for the production of food, feed, and fiber.

In Human Efficiency . . . Weeds such as poison ivy and ragweed that cause hayfever and other debilitating allergies contribute markedly to human misery and make necessary the annual expenditure of large sums for medical attention and for travel to noninfested areas during the hayfever seasons. In addition, many hours of manpower are lost.

In Other Areas . . . Propagation and survival of many harmful insects are favored by the presence of weeds on which they can breed and feed. For example, Russian thistle serves as an important food plant for migrating beet leafhoppers that transmit curly top virus to sugarbeets and vegetables. Weeds also serve as alternate hosts for many plant diseases such as wheat rust and parasitic nematodes which cause tremendous losses to agriculture each year.

Weeds on ditchbanks, on highway, railroad, and utility rights-of-way, in fence rows, and on other areas adjacent to cropland produce large quantities of seed and thus serve as reservoirs for invasion of fields through movement of seed by wind, water, man, and animals or by vegetative spread. Weeds in the above areas, as well as in lawns, parks, golf courses, playgrounds, cemeteries, and other public and privately owned areas, are unsightly and increase maintenance costs. Trees and other vegetation that obstruct and damage telephone and power

transmission lines are a particular problem, and weeds and brush on highway rights-of-way obstruct visibility and increase traffic hazards.

HERBICIDES AS PRODUCTION TOOLS

WE are entering an era of "chemicalization" in agriculture. Herbicides are used to kill weeds classified as pests; thus they are also referred to as "pesticides." But herbicides are more than pesticides, and more than crop protectants. They are crop production chemicals. Herbicides differ from other pesticides in that they can reduce the man-hours, machine-hours, and machine horsepower requirements in crop production. Their use also has far-reaching effects on other crop production and crop management practices. In effect, herbicides represent an additional production tool or source of energy for increasing farming efficiency and reducing horsepower and energy requirements on farms. And this is in accord with the meaning of the term "energy." For energy is defined as the capacity to perform work. In this context, herbicides are real work horses. How efficient are they? What is their capacity to perform work? Let's illustrate the principle with an example of chemical weed control.

Cost studies in cotton show that to control weeds in this crop by hoeing and cultivation requires 25 to 30 man-hours per acre per year at an annual cost of $15 to $20. The use of herbicides for weed control in cotton reduces the man-hours per acre to 8–12 and lowers the cost of weed control to $8 to $12 per acre. If we apply these per acre savings to the entire cotton crop, farmers would save more than $75 million each year. This is a striking example of the work-performing capacity of herbicides and points to the vast potential value of chemicals in improving farming efficiency.

SCOPE OF WEED CONTROL

MUCH of the energy and horsepower used on farms is for the purpose of moving more than 250 billion tons of soil each year, much of it several times in tillage and cultivation operations. This amount of soil would make a ridge 100 feet high and 1 mile wide from New York to San Francisco. This is the world's largest materials-handling operation and the energy required to perform this work is enormous. At least one-half of this vast tillage and cultivation operation is practiced solely for the control of weeds.

Nonchemical methods are used on about 80 percent of the national crop acreage and herbicides on about 20 percent. Approximately 140 million acres of intertilled row crops receive intensive weed control practices each year. More than 225 million acres of drilled crops receive moderate weed control practices. The intertilled row crops usually receive from two to five seedbed preparation treatments and from one to as many as seven cultivations in a single growing season.

Weed control practices are utilized on more than 1 billion acres of hay, pasture, and rangelands, millions of acres of nonagricultural lands, aquatic sites, and rights-of-way.

More than 200 million pounds of herbicides were used to control weeds on about 90 million acres of land in 1962 at a cost of more than $200 million.

The annual production of all synthetic organic pesticides, including herbicides, which were essentially unknown prior to 1940, has now reached a level of approximately 600 million pounds per year. Farmers are paying more than $500 million for these pesticidal chemicals each year, with a good net profit return on the investment.

In 1940 there were approximately 38 fungicides, 3 nematocides, 4 growth regulators, 14 herbicides, and 50 insecticides available for use on farms. Today farmers have a choice of 45 fungicides, 12 nematocides, 16 growth regulators, more than 100 herbicides, and over 250 insecticides. An effective and economical array of chemicals to stimulate, inhibit, and modify plants and animals and protect our crops and livestock from weeds, insects, diseases, and other pests is available for use by farmers. New agricultural chemicals with diverse properties for use in the production and protection of plants and animals are being introduced at an unparalleled rate.

Farmers have demonstrated outstanding interest in the use of chemicals to control weeds. About 70 percent of the acreage being sprayed for weed control is being treated by farmers with their own equipment. Custom operators are furnishing and applying the herbicides on the remaining 30 percent of the total acreage.

More than 16 million acres of corn were treated in 1959 at a cost of about $36 million. Chemical

weed control in corn eliminates two cultivations. Since each cultivation costs about $1.50 per acre, the benefits from reduced cultivations alone on 16 million acres are estimated at $12 million annually. Additional benefits are derived from reduced weed seed populations, improved harvesting efficiency, greater mechanized production, and higher yields and quality due to reduced weed competition for light, moisture, and nutrients.

In 1959 farmers sprayed more than 19 million acres of small grains, over 2 million acres of sorghum, more than 1 million acres of cotton, ½ million acres of soybeans, more than ½ million acres of rice, over ¼ million acres of vegetable crops, more than 2 million acres of pasture, 4 million acres of rangelands, and 2½ million acres of noncrop land. A 1962 USDA survey shows a striking increase in the crop acreage treated with herbicides since 1959.

A recent report published by the Minnesota State Department of Agriculture indicates some important trends in the expanding use of herbicides in that State for the past 8-year period. In 1950, there were 18,964 sprayers as compared with 40,927 in 1960. In 1950, Minnesota farmers sprayed 1,910,917 acres of grain crops, 13 percent of the total planted; while in 1960 (10 years later) they sprayed 6,171,508 acres of grain, 50 percent of the total grain crops planted in the State. This report also indicates that in 1960 over 55,000 miles of township, county, and State highway rights-of-way; 4,000 miles of railroad rights-of-way; 7,000 miles of powerline utility rights-of-way; and 3,000 miles of ditchbanks were sprayed for weed control.

EXPANDED SCOPE OF RESEARCH

AT least two yardsticks can be used to measure the progress in weed research. One is the increase in public funds appropriated to support research on weeds; the other is the improvement in the quality, diversity, and types of research.

Let us first consider funds.

Table 1 shows the increase in public funds directly supporting research on weeds in the United States

TABLE 1. PUBLIC FUNDS DIRECTLY SUPPORTING WEED RESEARCH IN THE U.S.

	Agricultural Experiment Stations			*Agricultural Res. Service*	
Fiscal Year	Federal Grant	Non-Federal	Total	USDA [1]	Grand Total
1950	$97,000	$526,000	$623,000	$181,283	$804,283
1951	141,000	560,000	701,000	176,071	877,071
1952	158,000	677,000	835,000	185,320	1,020,320
1953	166,000	745,000	911,000	228,678	1,139,678
1954	159,000	863,000	1,022,000	[2] 332,789	1,354,789
1955	302,000	970,000	1,272,000	361,400	1,633,400
1956	427,000	951,000	1,378,000	433,450	1,811,450
1957	540,000	1,106,000	1,646,000	[3] 660,660	2,306,660
1958	594,000	1,225,000	1,819,000	704,560	2,523,560
1959	636,000	1,164,000	1,800,000	728,170	2,528,170
1960	641,000	1,297,000	1,938,000	726,360	2,664,360
1961	693,000	1,540,000	2,233,000	1,018,800	3,251,800
1962	1,792,000	1,734,000	3,526,000	1,057,100	4,583,100

[1] Funds allocated for agricultural engineering research not included.
[2] Transfer of activities from U.S. Forest Service and Soil Conservation Service included.
[3] Transfer of activities from U.S. Department of Interior included.

from fiscal year 1950 through 1962. The total public expenditure for weed research in 1950 amounted to a little over $800,000; in 1962 it was $4,583,100, more than a fivefold increase. In the past 12 years ARS expenditures for weed research increased from $181,203 to over $1 million. In the same period expenditures by the State stations (Federal grant and non-Federal) increased in about the same proportion, from $623,000 to $3,526,000.

The increase in funds tells only a part of the story of progress in weed research. A more significant measure of progress is the upgrading, scope, and diversity of research currently underway.

In 1950 less than half the States were conducting weed research and this consisted mainly of the evaluation of herbicides. Such research, unless it is supported by appropriate soil and weather data, observations on ecological relationships and other pertinent information, does not yield results of maximum value. The same herbicide applied at the same rate on similar crops and weed species in different seasons may produce quite different effects that are difficult to explain, unless background information on environmental factors are available. Today there are 276 active weed projects among the 50 States and Puerto Rico. Each State has at least 1 weed project and some have as many as 18. Approximately half the projects are basic, dealing with biochemical and physiological problems, fate of herbicides in soils and plants, and ecological and life history studies. This research is designed to provide long-term answers to weed control problems.

One of the serious drawbacks in the development of better weed control practices is the lack of a complete understanding of the nature of weeds, the crop, or the herbicide. To understand all of the physiological aspects of a single herbicide requires the combined efforts of many scientists having different talents, training, facilities, and interests. Conclusions are often missed or are slow in being recognized when the investigators are not working as a team on the problem. A national and regional attack on the many aspects of weed control provides the added advantage of a team approach. Most of the U.S. Department of Agriculture weed research budget and approximately 10 percent of the expenditure for weed research at the State stations is on regional projects, directed toward the solution of problems of wide and important concern to two or more states. The projects are developed to use personnel and facilities to maximum advantage. They have well-defined and logically arranged objectives, pooled ideas on methodology with segments assigned to subcommittees, work groups, and individuals in order to expedite progress.

NE–42 Technical Committee in the northeast region has recently completed life-history studies on four weed pests—nutsedge, [*Cyperus* spp L.], quackgrass [*Agropyron repens* (L.) Beauv.], foxtail [*Setaria* spp (L.) Beauv.], horsenettle, Carolina [*Solanum* carolinense L.]—and is currently studying the life cycles of five other weeds—crabgrass [*Digitaria sanguinalis* (L.) Scop.], barnyardgrass [*Echinochloa crusgalli* (L.) Beauv.], dog fennel [*Eupatorium capillifolium* (Lam.) Small], yellow rocket [*Barbarea vulgaris* R. Br.], and smartweed [*Polygonum pensylvanicum* L.]. The weeds are being studied under different environments to determine the growth habits and the most susceptible stage of vulnerability to herbicides and control measures.

Western regional project W–52 is concentrating on finding the mechanism of action of important herbicides. Several of the States are working on the specific biochemical action of 2,4-D, one of the most widely used herbicides. The other project in the western region (W–63) is concerned with the effect of environmental factors on response of plants to herbicides. Research data correlate the influence of light, moisture, temperature, soil, and other environmental factors to the activity of various herbicides so that ultimate control can be described and predicated with a higher degree of accuracy.

The north-central region has just terminated a project in which factors affecting weed seed germination and bud dormancy were investigated. A new project was started in this region last year to study the nature and extent of the competitive relationships between crops and weeds.

The southern region is making a contribution in three phases of weed research: life cycle studies, physiological effects of herbicides on plants, and the fate of herbicides in soil.

ADVANCES IN FUNDAMENTAL PRINCIPLES

PROGRESS in chemical weed control during the past 10 years has been almost fantastic. Within this brief period many new chemicals and new weed control techniques were developed. These developments were highlighted by the discovery of the

herbicidal properties of the phenoxy compounds; the introduction of preemergence weed control; the development of low-pressure, low-gallonage application techniques; the development of preplanting chemical methods of control; the discovery of the role plants play in changing the structure, activity, and selectivity of herbicides; discovery of the effects surfactants, solvents, carriers, and other additives have on the selectivity, persistence, and fate of foliar and soil-applied herbicides; and the development of subsurface herbicide application techniques, soil-incorporation methods, and granular formulations of herbicides.

Herbicide Evaluation Research

SIGNIFICANT progress has been made during the past 10 years in developing and standardizing herbicide screening and evaluation techniques. Present methods of herbicide evaluation include the application of new chemicals as preplanting, soil-incorporated, preemergence, and postemergence treatments. Advances in experimental application equipment for utilizing extremely small quantities of experimental chemicals and the standardization of evaluation techniques gave impetus to the industrial discovery and development of new herbicides. The development of logarithmic application techniques is an outstanding example of designing a research tool to evaluate more accurately, efficiently, and rapidly the herbicidal properties of new chemicals.

The present tendency is to use a greater variety of herbicides and to use specific ones for the control of specific weeds in specific crops and special areas. The rate of development and some of the trends in the development of new herbicides offer almost unlimited potential for the selective control of weeds in almost any weed-crop situation.

An almost inexhaustible supply of chemical energy for the selective and nonselective control of weeds in a wide variety of weed-crop situations and specialized areas is provided by the substituted phenoxyacetic, phenoxypropionic, and phenoxybutyric acids; the substituted benzoic acids, phenylacetic acids, phenols, *N*-phenylcarbamates, thio and thiol carbamates, *N*-phenylureas, *s*-triazines; such herbicides as *N*-1-naphthylphthalamic acid [NPA], dalapon, 3-amino-1,2,4-triazole [amitrole], 2-chloro-*N*,*N*-diallylacetamide [CDAA], CDEC, and others.

Penetration, Absorption, and Translocation Studies

NUMEROUS factors influence the penetration, absorption, and the translocation of herbicides. Plant form, leaf shape, leaf position, leaf density, leaf surface, and leaf margins greatly influence the foliar distribution, retention, and uptake of herbicides.

Plants that have erect, spreading, or prostrate habits of growth with broad, large, narrow, and short or linear leaf shapes greatly influence herbicide recipient, distribution, and retention patterns. Plants with upright, horizontal, or pendulous leaves, which form foliage canopies of various densities, markedly influence the retention and uptake of herbicides.

The nature of the leaf surface is critically important. Leaves with waxy, hairy, or variously sculptured leaf surfaces differentially retain and absorb herbicides. Stomate distribution and the nature of the cuticle influence the quantity of material that penetrates the outer layers of the leaf. The permeability barriers of the cell membranes may further decrease the amount of chemical absorbed into the individual cells.

The form, shape, size, density, distribution, and other characteristics of roots in relation to soil-applied herbicides also partially determine the amout of herbicide that actually comes in contact with the plant.

Radioactive isotopes, gas chromatography, and other modern techniques are making it possible to obtain an improved understanding of the uptake and movement of herbicides in plants. Once the herbicide has been absorbed by the plant, it may be immobilized in the treated tissue by absorption to or conjugation with cell constituents. When certain herbicides are absorbed, the molecules are probably metabolized prior to translocation. Since foliar-applied herbicides move downward primarily in the phloem (living tissue) and soil-applied herbicides upward mainly in the xylem (nonliving tissue), all factors that influence plant growth and the transport of inorganic and organic solutes, and water and mineral elements also affect the movement of herbicides in plants.

The differential absorption and translocation of herbicides in different species often account for their selective action. For example, the intercalary meristem of certain grasses restricts the translocation of foliar-applied herbicides. Certain translocation

barriers also exist in perennial herbaceous and woody plants.

The mechanisms, energy concepts, and interrelationships of the translocation of herbicides in plants are not sufficiently understood for their most effective use. However, the development of new techniques for studying translocation and our present knowledge of herbicide movements in plants indicate that certain translocation obstacles prevent herbicides from reaching their sites of action in the cell in sufficient quantity to control plant growth. These same obstacles also influence and often determine the differential selectivity of herbicides. As we gain a fundamental understanding of the absorption and translocation of herbicides in plants, it will be possible to utilize more efficiently this knowledge for the development of highly selective chemicals.

Fundamental research on the penetration, absorption, and translocation of herbicides in plants has led to the development of new concepts regarding their formulation. In the early development of herbicides, primary emphasis was given to the chemical and physical properties of adjuvants that would preserve the herbicides in the container during shipment and enhance application with spray equipment. However, in recent investigations, increased emphasis has been given to the influence of surfactants, cosolvents, and other adjuvants on the selective action of herbicides on crop plants and weeds. It has been shown that surfactants may enhance the activity of a herbicide on certain weeds without increasing the activity of the same herbicide on certain crops. The results of these studies indicate that it will be essential to select surfactants and other formulating agents on the basis not only of the physical properties the surfactant contributes to the final formulation, but also of the role the surfactant plays in the differential activity and selectivity of herbicides on crops and weeds.

Recent investigations showed that surfactant carriers, cosolvents, and other adjuvants in herbicide formulations caused significant effects on the initial and residual activity of soil-applied herbicides. EPTC, formulated and applied in kerosene, was less persistent in soils than when acetone was used as a carrier.

Research has shown that formulation constituents can be used to modify the actions of herbicides for use in specific weed-crop situations. This fundamental knowledge adds to the growing arsenal of information that can be used in developing selective chemical methods of controlling weeds.

Sites and Mechanisms of Herbicidal Actions

HERBICIDES modify and control plant growth by inhibiting essential physiological processes or by preventing the biosynthesis of metabolites essential to plant growth. Some herbicides are known to kill weeds by inhibiting photosynthesis and essentially causing the cell to starve to death. Others may eliminate many of the biosynthetic reactions of the cell. Many herbicides inhibit enzymes that catalyze specific reactions. If inhibitions occur in a metabolic pathway, the plant may not be damaged if the growth factors blocked can be synthesized through other pathways. However, if a herbicide causes a metabolic block in specific pathways and the essential growth factors cannot be synthesized through other pathways, then growth becomes limiting and the plants may be killed.

While metabolism and biochemical syntheses of growth factors in plants undoubtedly play a significant role in the action of herbicides, the growth-controlling properties of herbicides are not necessarily limited to biochemical actions. Physical or chemical effects on cell membranes, spindle fibers, or other subcellular structures may disrupt normal physiological processes of these highly organized cellular components. Most herbicides are known to inhibit many biochemical or physiological processes. Control of plant growth with herbicides undoubtedly results from the accumulative effects of these many biochemical, metabolic, physiological, and physical inhibitions.

In 1904, beta-phenylpropionic acid fed to dogs was converted in their bodies to benzoyl glycine, a chemical with a different structure and different chemical and physical properties from that originally fed to the animals. This achievement was of great interest to plant scientists, but it was 1947 before they demonstrated that plants could also change the structure and activity of chemicals and that nonphytotoxic chemicals could be metabolized within plants to phytotoxic compounds. This important scientific breakthrough resulted in new concepts on the selective action of herbicides.

In 1954 it was shown that certain plants could metabolize the herbicidally inactive 4-(2,4-dichlorophenoxy)butyric acid [4-(2,4-DB)] through the

process of beta-oxidation to the herbicidally active 2,4-dichlorophenoxyacetic acid [2,4-D]. Therefore, weeds and crop plants capable of beta-oxidizing 4-(2,4-DB) to 2,4-D were killed, whereas plants not capable of beta-oxidizing 4-(2,4-DB) to 2,4-D were tolerant to the inactive 4-(2,4-DB) and were not killed. The highly selective herbicide 4-(2,4-DB) was developed directly as a result of these investigations. This herbicide has shown excellent promise for the postemergence control of broadleaved weeds in (*a*) cereal crops underseeded with certain forage legumes, (*b*) the establishment of pure stands of forage legumes, (*c*) forage legume seed production fields, (*d*) flax, (*e*) tolerant crop plants such as corn or rice grown in the vicinity of crops highly susceptible to the phenoxyacetic and alpha-phenoxypropionic acids such as cotton and grapes, and (*f*) certain other weed-crop situations.

Recent studies have also shown that plants can produce the opposite effect by changing a herbicidally active chemical into a nonphytotoxic one. 2-chloro-4,6-bis(ethylamino)-*s*-triazine [simazine], a very promising preemergence herbicide for weed control in corn, when absorbed by the roots of the corn plant, is converted to a nonphytotoxic form. Therefore, corn shows considerable tolerance to simazine. On the other hand, many important weeds do not effectively convert simazine to an inactive chemical. These weeds are highly susceptible to injury and are easily controlled by simazine. Thus the metabolic fate of simazine in plants is opposite to that of 4-(2,4-DB).

Another fundamental investigation showed that 2,2-dichloropropionic acid [dalapon] and several other chloro-aliphatic acids inhibit the enzymatic synthesis of pantothenic acid, a B-vitamin essential to plant growth. Pantothenic acid is made by an enzyme which couples beta-alanine to pantoic acid. This enzyme has been isolated. The herbicides were shown to be competing with pantoic acid. The response of plants to dalapon may be due to the temporary inhibition of pantothenic acid synthesis. This was demonstrated by supplying pantothenic acid to barley leaves. The exogenous source of pantothenic acid partly protected dalapon-treated plants against the herbicidal action of dalapon.

These are but a few examples of how fundamental research contributes to a better understanding of the sites and mechanisms of actions of herbicides. These investigations have provided the knowledge that plants also play a significant role in the selective action of herbicides. A basic knowledge of the sites and mechanisms of action of herbicides will enable scientists to synthesize new and even more effective selective herbicides.

Fate of Herbicides and Herbicide Residues in Plants and Soils

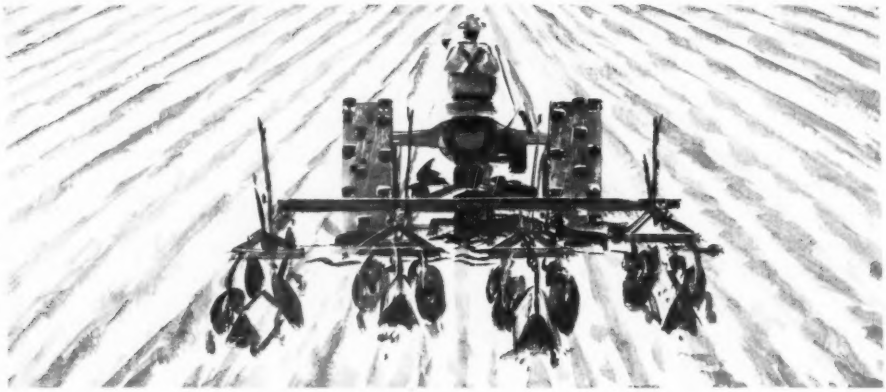
THE fate of herbicides in plants and soils is a critically important aspect of chemical weed control research in crop production. We must know their ultimate effects on the total environment. This represents an additional dimension in weed control research which must be more fully understood.

The fate of herbicides in plants is determined by morphological characteristics, physiological processes, and the biochemical properties of the protoplasm of plants as influenced by environmental and edaphic factors affecting plant growth.

Most herbicides can be recovered from plant tissue as the original molecules, even though major percentages of the compounds may have undergone changes in chemical structure. Consequently, we are not certain of the actual chemical structures through which many of the herbicides exert their growth-controlling actions. Conceivably some herbicides are applied in one form, translocated in a degraded or metabolized form, and cause inhibitions of growth at the site of action as yet another chemical structure. Other chemicals seem to be absorbed, translocated, and accumulated at the site of action as the original molecules.

Whether herbicides arrive at the site of action in plant cells as the originally applied molecules, or as degraded toxic metabolites, the accumulative evidence available today suggests that soil, morphological, translocation, physiological, and biochemical obstacles and their interaction with environmental and adaphic influences determine the selective action of herbicides by influencing the concentration of the herbicide that reaches the site of action at any one time. The sites of action in different species undoubtedly possess differential susceptibility to the toxicant.

The fate of herbicides in plants, animals, and soils is a relatively recent subject for scientific investigation. In view of the complexity of the subject, it is



not surprising that after 10 years of study we still know comparatively little about metabolism of herbicides in plants. Future research designed to uncover the principles, which determine how and in what form chemicals reach the growth sites involved in herbicidal action, will aid greatly in the solution of weed control problems. Implicit in such research is the need for more knowledge on how to use herbicides to provide optimum safety factors for economic crops, wildlife, and humans.

WEED CONTROL—A TOTAL FARM PROBLEM

IN attempting to determine how research may result in better weed control methods for more efficient crop and livestock production, it must be recognized that we are now entering a new era in the utilization of various forms of energy. Insofar as weeds are concerned, herbicides will be the sources of energy and they, rather than the machine with which they are applied, will perform the work. This does not imply that the need for mechanical equipment will be reduced. Quite the contrary. It means greater emphasis on specificity and accuracy in placing the chemical energy in the exact amount, in the exact place, and at the exact time for it to perform its maximum work.

We must keep in mind that weeds are a total farm liability and all crops grown on the farm are subject to their competition. In our future thinking and planning, we must give greater consideration to weed control problems on the farm unit rather than limiting research to the control of weeds in a single crop. The cost of controlling weeds in a single crop sometimes appears high because only that crop is being considered, rather than the total weed problem in all crops grown on the farm.

To obtain a better balanced and more efficient weed control program in crop production, farmers must be encouraged not only to use chemical weed control methods for controlling weeds in the current crop, but to place greater emphasis on supplementing this program by the rotational use of herbicides on all tolerant crops throughout the rotation according to recognized safety and conservation standards.

We also need to expand our studies on the possible rotation of different herbicides on the same crop grown continuously and to learn more about the efficiency of rotating different herbicides on different crops throughout the rotation. This practice will permit continuity in the use of chemical energy to control weeds.

Rotating different herbicides on the same crop grown continuously and full utilization of different herbicides on tolerant crops throughout a crop rotation will establish the sound principle of preventing undesirable shifts in the weed population. Moreover, this practice avoids an accumulation of herbicide residues in the soil, and provides for the full use of chemical energy in combination with cultural practices to reduce weed seed populations in the soil.

A LOOK AT THE FUTURE

THE accomplishments of State, Federal, and industrial weed scientists and their institutions are

often cited by agricultural leaders as an outstanding example of the progress that can result from a well-balanced, cooperative, and coordinated team effort. But the total potential of this new discipline is far from being reached. More emphasis is needed on every aspect of weed science: research, extension, regulation, and training and education including safe use. And a better correlation could exist between resources and actual losses—comparable to that in the control of insects and diseases.

There is much evidence to indicate that agriculture is on the horizon of a second-generation breakthrough in production efficiency because of the revolution in weed science. Already, the accomplishments made possible by this revolution have set in process the necessity for a new research cycle that can result in new plateaus of crop yields, crop quality, and production and harvesting efficiency.

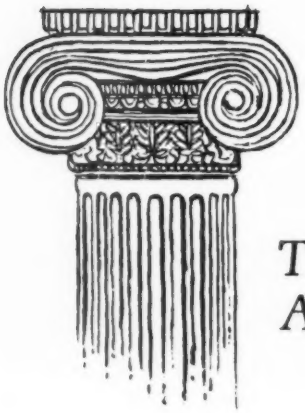
Of course no one would attempt to predict what new discoveries might develop in weed control from intensive fundamental and applied research involving chemistry, plant physiology, genetics, crops and soil science, and agricultural engineering. We can be certain, however, that unless fundamental and applied studies are brought into better balance and expanded, applied studies in the development of weed control practices in crop production will suffer. The use of herbicides in some instances is beginning to exceed the fundamental and applied research information available to insure their safe use. If a better balance between research in weed control and the use of chemicals is not obtained and maintained in the immediate future, the risk of damage to crops and all phases of the total environment will increase.

If a seed is to germinate, a number of environmental conditions must be met prior to germination. When basic research is inadequate, the shutoff period in scientific development is not as immediate and definite as with the germination of a seed but it is almost as certain in the long run.

Our weed control progress will certainly be characterized by the discovery, development, and utilization of more efficient forms of energy in the future. The adaptability of chemical energy for controlling weeds offers almost unlimited possibilities for improving the efficiency of weed control. Thus it seems that our future rate of progress will be largely determined by (*a*) the discovery of more selective, more specific, better translocated, more efficient, better formulated, safer, and more economical herbicides; (*b*) a fundamental understanding of the effects of chemicals on plant growth, soils, and the total environment including man, animals, and wildlife; (*c*) our ingenuity in supplementing and combining chemical and cultural practices; (*d*) a fundamental understanding of the limitations of our current weed control practices; and (*e*) the development of new and more effective weed control techniques and the discovery of more effective and more efficient sources of energy for selective weed control.

Acknowledgment

Since the literature on this subject is quite voluminous, the authors did not attempt to document individual citations. They recognize and gratefully acknowledge the work of all those who have contributed to the weed science literature used in preparing this review paper.



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